

BULLETIN
of **CARNEGIE MUSEUM OF NATURAL HISTORY**

**THE STRATIGRAPHICAL PALEONTOLOGY
OF THE TERTIARY NON-MARINE
SEDIMENTS OF ECUADOR**

GEOLOGY

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ABSTRACT

The stratigraphy of all the Andean Tertiary non-marine basins of Ecuador is described. The rich molluscan fauna (30 species of molluscs have now been identified) has been thoroughly revised and three new species described—*Diplodon (Ecuadorea) bristowi*, *Neritina loyolaensis*, *Paleoanculosa kennerleyi*. The

stratigraphical position of the previously described Ecuadorian faunas has been reinterpreted. Half of the species have been recorded from localities outside Ecuador, and with this evidence the chronostratigraphy of the non-Ecuadorian deposits has been critically reviewed.

PART 1. GEOLOGY

C. R. BRISTOW

INTRODUCTION

At the present day, Ecuador is divided into three physiographical regions—the relatively low-lying coastal belt (La Costa), the Andes, and the Oriente, which is the western part of the Amazon Basin within Ecuador. Despite their present day prominence the Andes are relatively young; fully marine, deep-water deposition took place along the length of the Ecuadorian Andes throughout Maestrichtian times, and at least locally during Middle and Upper Eocene times (Bristow and Hoffstetter, 1977:349–51; Henderson, 1979). It is not possible to date precisely the first major uplift of the Andes but it appears to have taken place before the Upper Oligocene Saraguro Formation¹. The Saraguro Formation consists of lavas, pyroclastics, ignimbrites, which are thought to have been deposited sub-aerially, and, locally, conglomerates; it has been dated by the potassium/argon method at 26 million years. By Miocene times, a number of fresh-water sedimentary basins were established throughout the length of the Andes of Ecuador. These are from north to south: Chota, Cuenca, Girón, Nabón, Loja, and Malacatos, of which the Cuenca, Loja,

and Malacatos are the best known. In the Oriente there is a thick cover of, at least in part, non-marine sediments (Curaray, Chalcana, and Pastaza formations), but they have not been described in detail and little is known of their fauna and flora.

In this account, details will be given of the stratigraphy and paleontology of all the Ecuadorian Tertiary non-marine Andean basins, together with an assessment of their respective ages. The fauna of the best known basin, Cuenca, is now known to contain several species which have been recorded from other South American localities. The ages assigned to the fauna and sediments of many of these other localities are speculative as there are no marine marker horizons within the sequences, and also because the true age ranges of the molluscs are unknown. It is only at Cuenca, where the fossiliferous sediments rest on a dated lava of Lower Miocene age, that a reliable oldest date can be given to the fauna. This, however, does not necessarily mean that a similar fauna elsewhere cannot be older than this date.

STRATIGRAPHY

CHOTA BASIN

This basin is best exposed on the south side of the Rio Chota in the Province of Imbabura.

The sequence commences with the Tumbatú Formation which rests unconformably on metamorphic rocks. The formation is divisible into three units of

which the lowest consists of some 90 m of conglomerates, sandstones, and red, green, and khaki shales. The only fossils found are plant fragments. The middle unit comprises about 1,000 m of pale-colored shales, locally bentonitic, thin (1 to 2 m) sandstones and beds of lignite; two thin shell beds (10 to 20 cm) are composed almost entirely of the gastropod *Liris* aff. *minuscula* (Gabb). The upper unit, about 230 m thick, consists principally of grey-

¹ The Ecuadorian names and their age ranges used in this account are those defined in Bristow and Hoffstetter (1977).

wackes, tuffaceous sandstones, and locally conglomerates, shales, and tuffs. Silicified wood is the only fossiliferous material. The Tumbatú Formation has a gradational junction with the overlying Chota Formation. The Chota Formation, some 144 m thick, is divided into four units of breccias and conglomerates, and unfossiliferous sediments.

Hall (*in*: Bristow and Hoffstetter, 1977:268) noted the similarity of the bentonitic shales and lignites of the middle part of the Tumbatú Formation to the similar lithologies of the Mangán Formation (Upper? Miocene) of the Cuenca Basin, and to the Arajuno Formation (Upper Miocene) in the Oriente. This similarity can be extended to the Curaray (Upper Miocene) and Upper Pastaza (Upper? Miocene) formations, also of the Oriente, and to the San Cayetano (Upper? Miocene) of Loja and Malacatos, and to the Nabón (Miocene) Formation.

The only fossil, *Liris minuscula* (Gabb), was described from Pebas, Peru. As discussed below, the age of the Pebas deposits are thought to be of Upper Miocene/Lower Pliocene age.

CUENCA BASIN

The Cuenca Basin is the largest and best known of the Andean Tertiary basins (Table 1). It has been studied by various workers from the time of Humboldt (1823). The most recent account is by Bristow (1973) and the following stratigraphic notes are based on that account. The paleontology is completely revised.

The early stratigraphy (Sheppard, 1934; Liddle, *in* Liddle and Palmer, 1941) was somewhat confused as it was not appreciated that the so-called "Cuenca Shales" were a hybrid deposit, with the similar lithologies of the Loyola, Guapán, and Mangán formations not stratigraphically distinguished. The correct sequence was first recognized by Erazo (1957) and this has been adopted, with minor nomenclatural changes, by subsequent authors. The evolution of the terminology, and the ages assigned to the various formations by differing authors is shown diagrammatically in Bristow (1973: fig. 2).

The sediments of the Cuenca Basin are strongly folded and faulted. In the area between Azogues and Cuenca where they are best known, the structure consists principally of a central north to south or northeast to southwest trending Biblián Anticline. On the east side of the anticline is the similar trending Azogues Syncline. West of the anticline as far as the Deleg Fault the sediments are steeply

dipping, or even overturned, but west of the Deleg Fault the strata are virtually horizontal.

North of Azogues the Biblián Anticline and Azogues Syncline cannot be recognized. The sediments are commonly steeply dipping, but faults are the dominant structural element.

In the center of the basin the contact with the pre-Tertiary formations is not seen; in the east the younger formations successively overlap the older to rest with marked unconformity on the Maestrichtian Yunguilla Formation.

The relationship of the Tertiary sediments to the older beds on the west side of the basin is obscure. The strata are weathered, not well exposed, and there is much superficial volcanic or glacial debris mantling the surface. The boundary may be faulted, or as in the east the younger sediments may have overlapped on to the older.

The Cuenca Basin has been mapped at a scale of 1:50,000. The major part of the outcrop falls on the two 1:50,000 Azogues (73 NW) and Gualaceo (73 SW) geological sheets (1974), published by the Dirección General de Geología y Minas, Quito; the northern part of the basin is included on the 1:100,000 Cañar (72) Sheet (1975); most of the remainder of the southwestern portion falls on the 1:100,000 Girón (1974) Sheet². All the localities mentioned in the text can be found on these sheets. The local grid references are taken from these same maps.

Biblián Formation

The formation crops out over some 40 km in the core of the main anticline, extending north-northeast to south-southwest from north of Biblián to near El Valle (740, 250) south-southeast of Cuenca. In addition there is a large isolated outcrop of similar trend to the east and this is seen from Jadán (360, 810) to the Quingeo area (300, 650) south of Santa Ana.

It was only the Biblián Anticline outcrop which was known to Sheppard (1934) and Liddle and Palmer (1941). However, the fossiliferous horizon within the "Biblián Sandstone and Conglomerate" locality of the above authors, exposed on the flanks of the small anticline (377, 990) between Biblián and

² The Girón Basin is separated from the Cuenca Basin by a blanket of Pleistocene volcanic deposits. Little is known of the deposits of this area—originally they were mapped as the undivided Ayancay Group (=Mangán + Santa Rosa Formation), but it is now thought that sediments of the Azogues and Mangán formations occupy the basin. The only fossil found to date is a juvenile *Neocorbicula* sp.

Table 1.—Stratigraphic column showing the composition of the Cuenca Basin, Ecuador.

STRATIGRAPHIC COLUMN OF THE CUENCA BASIN					
SYSTEM		FORMA- TION	GENERALIZED VERTICAL SECTION scale 1:30,000	LITHOLOGY	FOSSILS
PLEIST- OCENE		TURI		White, buff and pink silts; fine-grained tuffs and tuffaceous sandstone. Conglomerate.	Wood, mammoth
PLIOCENE		SANTA ROSA		Alternating sequence of pebble and boulder beds, with red silty and sandy shales Passage from Mangán Formation	
MIOCENE		UPPER	MANGAN	Alternating sequence of coarse brown tuffaceous sandstones, pebble beds and green silty shales	<i>Fossula derbyi</i> , <i>Neocorbicula cojitamboensis</i> , <i>Doryssa bibliana</i> , <i>Aylacostoma browni</i> , <i>Aylacostoma sulcata</i> , <i>Paleoanculosa kennerleyi</i> , <i>Neritina pacchiana</i> , <i>Vetustocytheridea bristowi</i> , <i>Hoplias sp.</i> <i>Paleoanculosa kennerleyi</i>
				Cañari coal seams	
				Alternating sequence of coarse brown tuffaceous sandstones, and red and green silty shales. More shaly towards the base.	
				Bentonite Washington coal seams	
				Hard white silica rock	
				Alternating sequence of coarse brown tuffaceous sandstones and buff and brown shales	
MIOCENE		MIDDLE	AZOGUES and GUAPAN	Buff fissile shales with bentonite	<i>Neocorbicula cojitamboensis</i>
				Coarse, buff tuffaceous sandstone with thin shale beds. Locally basal conglomerate	
MIOCENE		LOWER	LOYOLA	Buff fissile shale with occasional limestone lenses. Much gypsum veining.	<i>Diplodon guaranianus biblianus</i> , <i>D. bristowi</i> , <i>D. liddlei</i> , <i>Monocondylaea azoguensis</i> , <i>M. pacchiana</i> , <i>Erodona iquitensis</i> , <i>Pisidium sp.</i> , <i>Neocorbicula cojitamboensis</i> , <i>Ostomya fluviatilis</i> , <i>Calliostoma sp.</i> , <i>Neritina loyolaensis</i> , <i>N. pacchiana</i> , <i>Puperita sphaerica</i> , <i>Potera bibliana</i> , <i>Pomacea manco</i> , <i>Hydrobia ortonii</i> , <i>Lyrodes sp.</i> , <i>Doryssa bibliana</i> , <i>Aylacostoma browni</i> , <i>Gyraulus sp.</i>
				Argillaceous sandstones, coarse sandstones and conglomerates on east side of basin	
					BIBLIAN
				Unconformity	

Azogues, is in fact the overstepping basal bed of the Loyola Formation.

The base of the formation is not exposed in the core of the main anticline and it is possible there that it rests on older Tertiary strata at depth. In the isolated outcrop east of Cuenca the formation rests with marked unconformity on the Maestrichtian Yunguilla Formation. In this vicinity, where the Biblián Formation is not overlain by younger Tertiary sediments, the thickness exceeds 1,000 m. In the center of the basin there is a gradual upward transition over a few meters into the overlying Loyola Formation.

The basal bed of the Biblián Formation is a fairly coarse pebble bed often incorporating pebbles of the underlying Yunguilla Formation. Near Jadán (355, 813) an abundance of plum-red volcanic agglomeratic material occurs close to the Biblián/Yunguilla contact, and although the field relationships are not clear it appears to form a local base to the formation. In this general area coarse clastic units up to 30 m thick dominate the sequence, whereas it is more argillaceous in the Biblián-Azogues area. In this latter area the buff or light-brown, soft, tuffaceous sandstones, grits, and conglomerates occur in thinner lenticular units within the red and purplish-red silty and sandy shales which typify the formation. Locally, greenish-gray colors occur. There is much gypsum veining of the deposits.

As mentioned above, in the center of the anticline there is an upward passage into the Loyola Formation. In three localities at least, there are however andesitic volcanic deposits at, or very close to, the junction between the Biblián and Loyola formations. Thin andesitic lavas occur in at least two localities (352, 972) near Cojitambo in the uppermost part of the Biblián Formation. Cojitambo, which forms such a prominent landmark (see Plate 5 of Liddle and Palmer, 1941) has long been regarded as an intrusive andesite at the junction of the Loyola and Biblián formations. However, the contact with the overlying Loyola Formation shows little or no evidence of metamorphism, although Liddle and Palmer (1941:18) remarked that the shales were slightly baked. The general fine-grained aphanitic texture and the presence of volcanic glass in the matrix shows that it is in fact extrusive and probably contemporaneous with the El Shalal deposits described below. At El Shalal (360, 990) there is an outcrop of interbedded lavas, volcanic agglomerates, fine-grained tuffs and coarse tuffaceous sandstones and grits, which are well exposed along the Biblián-

Azogues road (see Plate 4, Fig. 2, of Liddle and Palmer, 1941) at the junction of the Biblián and Loyola formations.

At Descanso (368, 867) on the east side of the basin a fourth outcrop of andesite underlies the overstepping basal Loyola Formation. The base of the andesite is not seen, but the andesite does incorporate blocks of the Yunguilla Formation. The relationship of the andesite to those described above is not known, but it is thought to be a correlative of them. The outcrop at Descanso is regarded as the residual remnant of the highest Biblián Formation prior to its disappearance beneath the overstepping Loyola Formation. The significance of this andesite is that two Lower Miocene K:Ar age determinations of 19 and 20 million years ago have been obtained on samples from it (Snelling, 1974, unpublished report of the Institute of Geological Sciences, London). Regardless of its exact stratigraphic position, it means that the fossiliferous basal Loyola Formation which rests on the andesite cannot be older than uppermost Lower Miocene.

Fauna and age.—Only a very sparse fauna has been collected from this formation. The fossiliferous Biblián Sandstone and Conglomerate locality of Sheppard (1934) and Liddle and Palmer (1941) is the basal bed of the Loyola Formation and is fully discussed below. The author has found a thin shell bed composed almost entirely of *Doryssa bibliana* (Marshall and Bowles), but with rare *Diplodon guaranianus biblianus* (Marshall and Bowles) in the uppermost part of the Biblián Formation at only two localities near El Valle (250, 757; 278, 780) (loc. CRB 8 and 5). This sparse fauna is also known in the overlying Loyola Formation and since there is a passage from one formation to the other in the center of the basin accompanied only by a change of sedimentation and not by an orogenic break, there is thought to be no great time difference between the two formations. On this evidence the Biblián is regarded as of Lower Miocene age.

Repetto (1977) found a tooth in the lower (?) Biblián 8 km west of Azogues, of a notungulate toxodont, close to but distinct from *Prototoxodon rothi* Kraglievich of Middle Miocene age.

Sigal (1968) examined 64, and the author one, samples from the formation, but all proved to be barren of microfauna, other than reworked Maestrichtian foraminifera (*Rugoglobigerina* sp.) and ostracods.

Pollen recorded by Savoyat et al. (1970:57–60,

and Fig. 2) from the Biblián and Loyola formations, gave a Paleocene-Lower Eocene date to the Biblián, and a Lower-Middle Eocene date to the Loyola Formation. Because the sparse data of the Loyola Formation are so at variance with the radiometric age determinations, the palynological dating of the Biblián Formation is also thought to be grossly in error. If the pollen identifications are correct the palynology may be at fault either because the spores are derived, or because their true age ranges within Ecuador in particular, and South America in general, are not known with certainty.

Loyola Formation

The type locality is the small village of Loyola, also known as Chuquipata (373, 908), 7 km SSW of Azogues.

The formation has an extensive outcrop on the flanks of the Biblián Anticline. A thin, but important, outcrop occurs on the east side of the Azogues Syncline. North of Biblián the Loyola Formation is either faulted out or disappears beneath a younger deposit. A small fault-bounded outcrop is seen (368,163) to the south of Ingapirca.

The Cuenca White Shales of Sheppard (1934) were defined as occurring between the Biblián Sandstones and Conglomerates, and the Azogues Sandstone. By this definition they are synonymous with the Loyola Formation, but, from an examination of Sheppard's Fig. 2, it is clear that the Guapán Formation as now recognized was included within his Cuenca White Shales. Liddle (*in* Liddle and Palmer, 1941:22) also included the shales and coal of what is now known as the Mangán Formation in the Cuenca Shales. Additionally, the fossiliferous "Biblián Sandstone and Conglomerate" locality of Sheppard (1934) and Liddle and Palmer (1941) at the classic anticlinal section between Biblián and Azogues, is in fact the overstepping basal bed of the Loyola Formation. Erazo (1957:13-14) was the first to recognize much of the confusion, but no new names were given to the revised strata. These were eventually introduced by the United Nations (for example, UNDP, 1969).

The dominant lithology of the formation consists of a monotonous sequence of fissile dark gray shales and silty shales which weather buff or cream. Locally, lenses of limestone occur together with thin layers of soft sandstone. Gypsum veining and coatings to joints and bedding surfaces is a common feature of the weathered rocks. In the center of the

basin the Biblián passes upward, with no marked break, into these fissile shales. Fossils, other than fish remains and leaves, are uncommon but local shell beds composed almost entirely of *Doryssa bibliana* occur.

On the eastern side of the basin there is a well-developed basal series of sandstones and conglomerates. It is possible to trace a gradual overstep of the Loyola Formation across the Biblián Formation and on to the Yunguilla Formation. This is well seen between Descanso (368, 867) and a point (410, 953) south of Azogues, and at the historically important road and railway cuttings in the small-scale anticlines and synclines to the northwest of Azogues (377, 990). At this latter locality the basal beds are some 45 m thick. The pebbles of the conglomerates consist of tuff, quartzite, quartz, and fragments of the Yunguilla Formation. At Descanso, where these beds rest on andesite, much weathered angular andesite is incorporated in it. The basal beds are locally richly fossiliferous and have yielded the principal faunas. Fossils consist dominantly of molluscs, but crustacean debris, fish teeth and scales, ostracods and charophytes are common.

The maximum thickness of the formation is about 360 m in the center of the basin.

Flora, fauna, and age.—Until recently the fauna of the Cuenca Basin was thought to be endemic (Marshall and Bowles, 1932; Liddle and Palmer, 1941). Parodiz (1969) first demonstrated that certain species did occur outside Ecuador. Further collecting extended the number of non-endemic species (Bristow, 1973). This new fauna, together with additional molluscan material collected during 1974 has been completely revised by Parodiz and the results incorporated here.

The known fossils from the Loyola Formation include:

Plants

Gymnospermae

Trigonia varians Engelhardt (CRB 18)
(Berry, 1934, 1945)

Macrolobium tenuifolium (CRB 18)
Engelhardt (Berry, 1934, 1945)

Charophytes

Chara sp.

Pollen—various spores listed by Savoyat et al. (1970:57-60, fig. 2), but of doubtful value (see below)

Mollusca

Bivalvia

<i>Diplodon (Ecuadorea)</i> <i>guaranianus biblicianus</i> (Marshall and Bowles)	CRB 18, 28
<i>Diplodon (Ecuadorea)</i> <i>bristowi</i> , new species	CRB 18
<i>Diplodon (Ecuadorea) liddlei</i> (Palmer)	CRB 7, 18
<i>Monocondylaea azoguensis</i> (Palmer)	CRB 18
<i>Monocondylaea pacchiana</i> (Palmer)	(CRB 18)
<i>Monocondylaea</i> sp.	CRB 18
<i>Anodontites olssoni</i> (Palmer)	CRB 18
<i>Pisidium</i> sp.	CRB 7, 11, 26, 46
<i>Neocorbicula cojitaubensis</i> (Palmer)	CRB 6, 7, 9, 10, 11, 15, 18, 26, 34, 48, 49
<i>Erodona iquitensis</i> (de Greve)	CRB 7
<i>Ostomya</i> cfr. <i>fluviatilis</i> (H. Adams)	CRB 26
Gastropoda	
? <i>Calliostoma</i> sp.	CRB 7
<i>Neritina loyolaensis</i> , new species	CRB 9
<i>Neritina pacchiana</i> (Palmer)	CRB 34
<i>Neritina</i> sp.	CRB 7
<i>Puperita</i> aff. <i>sphaerica</i> (Olsson and Harbison)	CRB 18, 46, 48
<i>Poteria (Pseudoaperastoma)</i> <i>bibliciana</i> (Marshall and Bowles)	CRB 26, (18)
<i>Pomacea (Limnopomus)</i> <i>manco</i> Pilsbry	CRB 34
<i>Hydrobia ortonii</i> (Gabb)	CRB 7, 11
<i>Lyrodes</i> sp.	CRB 7
<i>Potamolithoides biblicianus</i> (Conrad)	CRB 26b, (18)
<i>Aylacostoma browni</i> (Etheridge)	CRB 18
<i>Aglacostoma dickersoni</i> (Palmer in: Liddle and Palmer, 1981)	
<i>Doryssa bibliciana</i> (Marshall and Bowles)	CRB 2, 12, 14, 17, 18, 28

Pulmonata

<i>Gyraulus</i> sp.	CRB 7
<i>Succinea</i> sp.	CRB 7

Crustacea

Ostracoda

<i>Vetustocytheridea bristowi</i> Bold	CRB 11, 26, 27, 30, 35, 42, 51
-------------------------------------------	--------------------------------------

Brachyura

<i>Necronectes proavitus</i> Rathbun (Bristow, 1973; Collins and Morris, 1976)	CRB 26
--------------------------------------------------------------------------------------	--------

Echinoidea

Unsubstantiated record (Erazo, 1965:9)	CRB 26
-------------------------------------------	--------

Fish

Characoids

<i>Hoplias</i> sp., <i>Leporinus</i> sp. (Roberts, 1975)	CRB 7, 9, 10, 11, 18, 26, 30, 31, 51
-------------------------------------------------------------	-----------------------------------------------

Parentheses signify material described by previous authors in same localities (CRB) recollected by the author.

Arenaceous foraminifera recorded from the basal beds of the Loyola Formation (Bristow, 1973) are almost certainly derived from the underlying Yunguilla Formation (J. Whittaker, personal communication). The calcareous Miocene ?*Siphogenerina senni* also listed in Bristow (1973) is now regarded as a contaminant. *S. senni* occurs in the marine Miocene coastal deposits of Ecuador and samples from the coastal provinces were being processed at the same time as the author's samples.

With one exception, there is little in this fauna to provide an accurate independent date, but collectively a Miocene age is indicated. The following inferences can be made.

The leaves recorded by Berry (1934, 1945) also occur in the Miocene Loja Basin where the flora has been studied in greater detail (see below).

Chara sp. indicates a post-Middle Eocene, but more probably an Oligocene age (Grambast, personal communication).

The spores listed by Savoyat et al. (1970) are supposedly of Lower to Middle Eocene age. These dates are wildly at variance with the other evidence and are not accepted by Bristow (1973). (See remarks about the pollen of the Biblián Formation.)

Diplodon (Ecuadorea) guaranianus biblicianus is also known in the Miocene Monagas Series of Venezuela (Parodiz, 1969).

Pomacea (Limnopomus) manco occurs in the Upper Oligocene or Lower Miocene strata in Peru (Pilsbry, 1944).

Hydrobia ortonii is known from Iquitos and Pebas (de Greve, 1938).

Aylacostoma browni, which is also known in the Mangán Formation, is one of the more widely distributed species outside of the Cuenca Basin. Elsewhere it is known in ?Pliocene beds at Canamá, Brazil (Etheridge, 1879), and the ?Pliocene La Tagua beds, Colombia (C. P. Nuttall, personal communication).

Puperita sphaerica was first described from the Pliocene of Florida (Olsson and Harbison, 1953).

Although *Vetustocytheridea bristowi* is endemic to the Cuenca Basin, other members of the genus and allied genera (cf. *Cyprideis stephensoni* in the Malacatos Basin) are generally regarded as indicative of the Miocene.

Necronectes proavitus is the species which probably provides the best independent date for the Loyola Formation. The type specimen came from the Middle Miocene Gatun Formation. It is also recorded from the Middle Miocene of Puerto Rico (Gordon, 1966:184) and the Middle Miocene Brasso Formation of Trinidad (Collins and Morris, 1976:125). This Middle Miocene date is in close agreement with the Lower Miocene radiometric dates of 19 and 20 million years ago obtained on the andesite at Descanso which is immediately overlain by the crustacean-rich (not specifically identified at this locality) basal pebbly beds of the Loyola Formation.

Azogues Formation

There has been a gradual restriction in the application of the name 'Azogues' to the Cuenca sediments. Wolf (1879, 1892) used the term "Azogues Sandstone" for all the sediments of the Cuenca Basin. Sheppard's (1934:361) use of Azogues Sandstone was for the post-Cuenca White Shales (Loyola Formation). Liddle (*in* Liddle and Palmer, 1941:23) used the modified term "Rio de Azogues Sandstone," as the outcrops on the east side of the Rio Azogues (=Rio Burgay on modern maps) offered a better type locality. Erazo (1957) further restricted the Azogues Sandstone to those beds between the underlying Cuenca Shale (=Loyola Formation) and the (unnamed) overlying Guapán For-

mation. This restriction is logical, but it now means that the town from which the formation takes its name does not overlie it; Azogues is sited on the Guapán Formation. Subsequent authors have adopted Erazo's usage, although Liddle's name "Rio de Azogues Sandstone" would have been more applicable.

The Azogues Formation is best developed on either side of the Azogues Syncline where it extends from just north of Azogues in the north, to near El Valle (266, 750) in the south. On the west side of the Biblián Anticline the Azogues Formation extends from a short distance north of Cojitambo, southwards to Boquerón (230, 740) where it disappears beneath the unconformable Turi Formation. Southwestwards of Boquerón the Azogues Formation reappears but has been mistakenly grouped with the Mangán Formation and the two deposits have been mapped as the undivided Ayancay Series (1:100,000 Girón geological sheet). The disappearance of the formation north of Cojitambo is attributed to faulting, but it may be due to facies change.

The base of the formation is transitional over some 10 to 20 m with the underlying Loyola Formation. The dominant lithology is medium to coarse-grained, brown weathering tuffaceous sandstones, but beds of siltstone, clay, and shale occur, generally not more than 1 m thick and principally in the lower part. A characteristic feature of the sandstones is their curved weathering surfaces. The siltstones are generally off-white to pale yellow, have fine regular ferruginous laminae in places, and are of varying hardness. The shales are usually off-white to pale gray or yellow, locally slightly silty, usually poorly laminated and medium hard.

On the east side of the basin the Azogues Formation oversteps the older beds to rest directly on the Yunguilla Formation. In the area to the north and east of Azogues where the older Tertiary sediments are absent there is a well-developed basal conglomerate. At such points (for example, 402, 994), and along the road from Azogues church to Uchupucum (416, 985), the conglomerate is well exposed. Conglomerates, often with distinct cross bedding, are also developed at other levels. Well-rounded pebbles from 1 to 10 cm diameter, consist mostly of weathered igneous rock, with pebbles of quartz, and Yunguilla shales and limestone. The higher beds of the Azogues Formation in the syncline to the east of Paccha (304, 800) consist of volcanic agglomerate with pumice fragments.

Where the Guapán Formation is developed in the

Azogues Syncline the junction with the Azogues Formation is interdigitational over a few meters. The Guapán Formation appears to be a lateral facies of the Azogues Formation, as a thickening of either is accompanied by a thinning of the other. Where the Guapán Formation is absent, and the Mangán Formation directly succeeds the Azogues Formation, the contact between the two formations is also transitional, but over a somewhat greater thickness of beds than with the Guapán.

The maximum thickness appears to be about 280 m in the El Tablón vicinity (265, 792), some 4 km east of Cuenca.

Fauna and age.—Fossils have not previously been found in the Azogues Formation. Sheppard's (1934:362–363) Paccha samples clearly came from the Loyola Formation (see his Fig. 4) while his material from the Biblián Sandstone and Conglomerates (=basal Loyola Formation) he confusedly includes within the Azogues Sandstone. Fossils found by Olsson (*in* Liddle and Palmer, 1941:24) said to be from this formation between Puente del Descanso and Cerro Tuhual are almost certainly from the basal Loyola Formation (=CRB 9). The somewhat doubtfully identified *Nucula* cf. *andersoni* Clarke recorded from the base of the formation (UNDP, 1969:15), and the marine fossils found by Erazo (1965:9) also come from the condensed basal beds of the Loyola Formation. Thirty-two samples collected by Sigal (1968) were barren of microfauna.

The author has collected a limited, but significant, fauna from the basal beds of the Azogues Formation at three localities (CRB 1, 305, 835; CRB 4, 258, 786, and CRB 13, 308, 832). *Neocorbicula cojitamboensis* occurred abundantly at all three localities. Additionally, *Aylacostoma* cfr. *dickersoni* and *Diplodon* sp. were present at CRB 1.

A. dickersoni is known from only one other locality—in the beds of the Loyola Formation on the southwest side of Cojitambo (Liddle and Palmer, 1941:36, map).

In view of the transitional contact with the Middle Miocene Loyola Formation, and as there is no distinct faunal difference between the two formations, the Azogues Formation is also regarded as Middle Miocene.

Guapán Formation

Because of lithological similarity, earlier workers had confused this formation with the older Loyola Formation (for example, Sheppard, 1934: Fig. 2). Erazo (1957:13–14, section 2) first recognized this

discrepancy but gave no name to the formation. The name "Guapán," taken from the outcrops near the Guapán cement works (394, 996), was introduced by the United Nations (for example, UNDP, 1969).

The formation is confined almost entirely to the center of the Azogues Syncline; a small isolated outcrop occurs on the west side of the Biblián Anticline in the area between Ayancay and Cojitambo (339, 892–346, 930).

The junction between the Guapán and Azogues formations is gradational and, as mentioned above, although the Guapán Formation overlies the Azogues Formation it also passes laterally into it.

The Guapán Formation consists characteristically of finely laminated dark brown to black shales, weathering white or yellow and with much limonite staining. The laminae tend to be thicker than in the Loyola Formation, but otherwise the two formations are very similar. Tuff and tuffaceous sandstones were noted on the roadside (385, 925) just south of Charasol and have been recorded in the lower half of the Guapán Formation near Ayancay. Sands, sandstones, and occasional conglomerates occur. Bentonite is known at Charasol (Nuñez del Arco, 1971). Also in this locality a gypsum seam was located some 60 m above the base of the formation.

The maximum thickness appears to be about 100 m in the center of the syncline.

Flora, fauna, and age.—Excellent preserved impressions of fossil leaves abound at many horizons, but await a detailed study. Fish scales are common; one incomplete characoid fish cf. *Moenkhausia* has also been recorded (Bristow, 1973). Seventeen samples taken by Savoyat et al. (1970) for microfauna proved to be barren.

In view of its facies relationship with the Azogues Formation, the Guapán Formation is thought to be also of Middle Miocene age.

Mangán Formation

The formation takes its name from the several localities to the west of Nazón (310, 010) which incorporate Mangán in their title. It is an unfortunate choice of name because all the localities overlie the Santa Rosa Formation.

The Mangán Formation has a wide and extensive outcrop on the west side of the Cuenca Basin from Ingaprica (365, 190) in the north, where it appears from beneath the Tarqui Formation, to just south of Cuenca where it disappears under the Turi Formation. Southwest of Turi where the Tertiary sed-

iments reappear in the area of the Girón Sheet (1974) they have been mapped as the undivided Ayancay Group (Mangán and Santa Rosa formations). They extend southwards as far as a point about 25 km NW of Saraguro. However, as mentioned above, the Ayancay Group as mapped in this area is misnamed, as the sediments comprise, at least in part, the Azogues and Mangán formations.

The coal-bearing strata of the formation have been known for many years, and were included in the upper part of Wolf's "Arenisca de Azogues." Liddle (*in* Liddle and Palmer, 1941) thought that they were part of the Cuenca Shales. Erazo (1957) was the first worker to separate off from the "Azogues Formation," the strata later to be named the Ayancay Group, but to which he gave no name.

There has been much research into the coal of the Cuenca Basin, of which the most recent and complete is that by the United Nations (UNDP, 1969). For that report the coal field was mapped at 1:10,000 scale and a considerable amount of detail exists for the quantity and quality of the coals, and for the structure of the coal-bearing deposits (see also Putzer, 1968).

For descriptive purposes it is convenient to divide the Mangán Formation into three units—a lower, including all the strata up to, but excluding, the lower (Washington) coal seams; a middle unit comprising everything from the Washington to the Cañari coal seam; and an upper unit above the Cañari seams. These three divisions can only be recognized in the area where the coal seams are developed.

There appears to be a transitional upward passage from the Azogues Formation, or from the Guapán Formation where present, into the Mangán Formation. The upper part of the Azogues Formation loses its massive sandstone beds, and red and green blocky shales appear, alternating with thinner sandstones. This alternating sequence characterises much of the Mangán Formation. The United Nations (UNDP, 1969), however, claims that there is a disconformity at the base of the Mangán, but there appears to be little evidence of this unconformity in the field. In the Cushumaute area (338, 954) the beds consist predominantly of light-colored siltstone, shale, and fine-grained sandstones, interbedded in layers generally less than 1 m thick.

The maximum thickness of this unit appears to be 870 m in the San Nicolás area (340, 940).

The gastropod *Paleoanculosa kennerleyi*, new species, found in a 10 cm seam (338, 953) in the

lower third of the unit near Cushumaute, scarce fish teeth from this same bed (Roberts, 1975:263), and leaves found stratigraphically below (339, 954) have been the only fossils found to date. The occurrence of a shell bed also composed entirely of the above gastropod near Ingapirca (365, 161), in an area where the Mangán Formation cannot readily be divided into three units, may indicate a potential stratigraphical marker for the lower Mangán Formation. The latter locality, where the road to Ingapirca crosses the Rio Cañar, is probably the same locality as that at which Reiss (see Wolf, 1892:257) found fossils. The Mangán Formation at this locality is in fault contact to the east with the Loyola Formation.

The middle unit is characterized in the center of the basin by the presence of several coal seams at its top and bottom. The Washington seams do not extend beyond the Rio Sidcay (290, 840) in the south, and the Cañar seams are here contaminated with clastics. Neither is well developed north of Nazón (330, 015) (UNDP, 1969:18).

Thick beds of shales, lithologically identical to those of the Loyola and Guapán formations, are well developed only in the lower part of the unit in close association with the Washington coal seams. Bentonite, in beds up to 15 m thick, has been noted at several localities. Higher in the sequence there is a well-bedded series of tuffaceous sandstones, silts, thin conglomerates, and thin shales. A conspicuous, persistent bed some 2 m thick of hard white, almost pure silica rock, first noted by Wolf (1892), occurs some 20 to 30 m below the Cañari seams and forms an excellent marker horizon. A similar bed above the Cañari seams was also noted by the United Nations (UNDP, 1969). Dark green tuffs have been recorded at the San Luis mine (334, 977). The coal seams, of sub-bituminous C grade, are "lenticular, sheared, faulted and otherwise unpredictably discontinuous." Other unfavorable factors, such as the near vertical foot and hanging walls, led to the closure of the last large-scale working mine, San Luis, in 1967 (UNDP, 1969:42). The maximum thickness of the middle unit appears to be 600 m.

All the fossils so far found within the formation, with the one exception in the lower unit mentioned above, are associated with the coal seams: directly over one of the Washington coal seams at Cochahuacu (335, 995), and in a similar position close to the San Luis mine (334, 976). Crocodile teeth and other vertebrate remains have been reported from

the coal seams (UNDP, 1969:18). The fossils are listed below.

The upper unit consists principally of coarse brown tuffaceous sandstones, commonly pebbly and becoming increasingly conglomeratic upwards. The arenaceous and conglomeratic beds alternate with blocky weathering green and brick-red silty clays. In the area (270, 865) north of Ricaurte, the passage into the overlying Santa Rosa Formation is gradational, but represented by a coarsening upward sequence and the incoming of red beds. In the Nazón area the change is more abrupt and much coarser conglomerates typify the Santa Rosa Formation.

The full thickness of the upper unit is unknown as nowhere is there a complete unfaulted sequence; it certainly exceeds 700 m. No fossils have been found in this unit.

Flora, fauna, and age.—The flora consists of well-preserved, but as yet unstudied, impressions of leaves.

Spores from the coal seams have been examined by Grebe (*in* Putzer, 1968:479–480, 486–487). They indicate a correlation between the Washington seams of the Cuenca Basin with the coal seams of the Loja and Malacatos basins.

The fauna is dominated by molluscs and includes the following:

Bivalvia

<i>Fossula</i> cf. <i>derbyi</i> Ihering	CRB 36b
<i>Neocorbicula cojitamboensis</i> (Palmer)	CRB 36a, 42c

Gastropoda

<i>Doryssa bibliana</i> (Marshall and Bowles)	CRB 36a
<i>Aylacostoma browni</i> (Etheridge)	CRB 36b, 42c
<i>Aylacostoma sulcata</i> (Conrad)	CRB 42c
<i>Neritina pacchiana</i> Palmer	CRB 36b
<i>Paleoanculosa kennerleyi</i> , new species	CRB 20, 60

Additionally, the ostracod, *Vetustocytheridea bristowi* Bold, has been found in sample CRB 42c, and jaw teeth of the erythrinid fish, *Hoplías* sp., have been found in sample CRB 36a (Roberts, 1975:263).

The fauna contains a mixture of species known from the underlying Loyola Formation, and several new species (*Fossula* cf. *derbyi*, *Paleoanculosa kennerleyi*, *Aylacostoma sulcata*). Of the new species for

this fauna, *F.* cf. *derbyi* was described from specimens from strata at Santa Maria do Boca do Monte, Rio Grande do Sul, Brazil. The age of the strata is uncertain. Ihering (1907) thought they were of Cretaceous age, but Parodiz (1969:83) was of the opinion that they were Upper Tertiary. *A. sulcata* is known at Pebas (Conrad, 1871), Pichua (Woodward, 1871), and Iquitos (de Greve, 1938).

In view of the occurrence of species common to both the Loyola and Mangán formations, including *Vetustocytheridea bristowi* thought to be indicative of the Miocene, the Mangán Formation is also regarded as Miocene. However, the vast thickness of sediments, approximately 1,800 m, separating the two formations suggests a significant time interval between them. The Mangán Formation is accordingly regarded as Upper Miocene in age.

Santa Rosa Formation

The uppermost formation of the Tertiary sediments of the Cuenca Basin consists predominantly of coarse clastic units alternating with red silty and sandy shales. They crop out on the west side of the basin. There appears to be an upward transition from the Mangán Formation. The contact with the overlying Turi Formation appears also to be transitional, at least in the center of the basin. Very coarse boulder beds in the Nazón area (362, 015) are probably indicative of proximity to their source area. The maximum thickness at outcrop appears to be about 500 m.

No fossils have been found in the formation and only a speculative Pliocene age can be assigned to it.

Turi Formation

Succeeding the Santa Rosa Formation in the center of the basin is a series of well-bedded, generally horizontal, conglomerates, volcanic breccias, ashes, shales, and sandstones. In the type area (214, 771) to the south of Cuenca, and in the central portion of its outcrop, there is a well-developed basal conglomerate. Around Turi the formation rests unconformably on the Loyola and Azogues formations, but further west there appears to be a transitional upward passage from the Santa Rosa Formation.

North of Biblián there is much volcanic debris in the formation which has expanded in thickness from approximately 280 m at the type locality to approximately 1,200 m. In this northern sector of the basin the sediments are steeply dipping.

The only fossils found to date are unidentified gastropods, silicified wood, and a possible mammoth bone (Erazo, 1957:28). The age is considered to be Pleistocene.

The Turi Formation is succeeded by a series of volcanic deposits (Tarqui Formation and Llacao Volcanics), till, terrace gravels, and alluvium. The Tarqui Formation provides the only independent date for the minimum age of the sediments of the Cuenca Basin. At two localities, carbonized wood fragments gave C^{14} dates of $24,900 \pm 1,200$, and $34,300 \pm 1,950$ BP (UNDP, 1969:22, 1972:13).

Sample sites

(Cuenca Basin)	Local grid references	Formation
CRB 1	305, 834	basal Azogues
CRB 2	311, 832	high Loyola
CRB 4	258, 786	basal Azogues
CRB 5	287, 780	uppermost Biblián
CRB 6	356, 846	basal Loyola
CRB 7	357, 842	basal Loyola
CRB 8	250, 757	high Biblián
CRB 9	367, 867	basal Loyola—Descanso section; Loyola Formation rests on lava radiometrically dated at 19 and 20 million years ago
CRB 10	370, 870	basal Loyola
CRB 11a	361, 855	high Loyola
11b, c	361, 855	middle Loyola
CRB 12	311, 832	high Loyola
CRB 13	308, 882	basal Azogues
CRB 14	311, 832	high Loyola
CRB 15	400, 923	basal Loyola
CRB 17	378, 915	high Loyola
CRB 18	378, 987	basal Loyola—"Biblián sandstone and conglomerates" locality of Marshall and Bowles (1932); loc. 1038 of Liddle and Palmer (1941)
CRB 20	337, 953	lower unit of Mangán
CRB 26	406, 947	basal Loyola—"echinoid" locality of Erazo (1965)
CRB 28	373, 016	basal Loyola
CRB 30b	245, 773	high Loyola
CRB 34	398, 912	basal Loyola
CRB 35	400, 918	basal Loyola

CRB 36	333, 976	middle unit of Mangán
CRB 39	179, 663	"Ayancay Group" of Girón Basin
CRB 42	332, 994	middle unit of Mangán
CRB 46	400, 929	basal Loyola
CRB 48	400, 929	basal Loyola
CRB 49	400, 929	basal Loyola
CRB 60	365, 161	Mangán
CRB 61	368, 159	Loyola

NABÓN BASIN

Nabón is a village about 50 km south of Cuenca and 75 km north-northeast of Loja. The deposits of the basin, the Nabón Formation, crop out over an area 16 by 6 km, and rest unconformably on the Oligo-Miocene Saraguro Formation. The general strike of the formation is northeast to southwest. The formation is divided into three units—a lower one, some 40 m thick, of bedded tuffs; a middle one, 130 m thick, of conglomerates, sandstones, siltstones, shales, diatomites, lignites, and minor tuffs; and an upper unit, 160 m thick, of bedded tuffs and agglomerates. The presence of lignite has been taken by most authors to indicate an equivalence with the coals of the Mangán Formation of the Cuenca Basin, and the San Cayetano Formation of the Loja and Malacatos basins. This is supported by the limited flora found in the middle unit which is also known from Loja (Bristow, 1976:107). Additionally, the rodent *Olenopsis aequatorialis* of uncertain stratigraphic provenance, was described from Nabón (Anthony, 1922). *O. aequatorialis* is common in the Miocene of La Venta in Colombia (Fields, 1957). At the time of writing, Fields regarded the La Venta sediments as Upper Miocene in age (Vindobonian/Friasian). These stages are now regarded by modern authors (for example, Van Eysinga, 1975) as part of the Middle Miocene. To date, no Mollusca have been found in the Nabón Formation. A tentative Middle-Upper Miocene date is hereby given to the Nabón sediments.

LOJA AND MALACATOS BASINS

These two separate basins have been studied by numerous authors, of whom the most recent is Kennerley (1973; 1:100,000 Loja, 1975, and Gonzanama, 1975 sheets). Initially Kennerley (1973) gave separate formational names to the similar deposits in each of the basins, but later, on the Loja and Gonzanama sheets, the stratigraphical nomenclatures of

the two basins were united and the following formational names, in ascending order, are currently in use: Loma Blanca, Trigal, San Cayetano, and Quillollaco.

Loma Blanca Formation

The type locality is a hill (895, 338) 4 km west of Malacatos. It is a volcanic formation comprising a well-developed basal agglomerate, succeeded by tuffs and agglomeratic tuffs. In the Loja Basin andesitic and basaltic lavas occur. It rests unconformably on older formations.

No fossils have been found in the formation. Kennerley (1973:29) thought that it was possibly equivalent to the Saraguro Formation. At the time Kennerley was writing the Saraguro Formation had not been dated, but it is now known to be of Oligo-Miocene age (26 and 28 million years ago, Snelling, *in* Bristow, 1976:107).

Trigal Formation

The name is taken from the Rio Trigal (963, 613) some 4.5 km northwest of Loja, where there are excellent outcrops. It crops out as a narrow belt on the west side of the basin where it rests unconformably on the Loma Blanca Formation. The dominant lithology is coffee-colored shales and clays; gypsum is common as a coating to bedding surfaces and joints.

In the Malacatos Basin the Trigal (formerly Algarobillo) Formation overlies the Loma Blanca Formation conformably. The lithology is similar to that of Loja but with minor beds of sandstones, tuffs, and in the upper part, thin seams of coal.

The presence of the ostracod *Cyprideis stephensoni* (Sandberg) in one sample from the Malacatos Basin, dates the formation as Miocene.

San Cayetano Formation

The type locality is the village of the same name (003, 596) 1 km north-northeast of Loja. The formation crops out extensively in the center of the Loja Basin, and as two belts in the Malacatos Basin. In both basins there is a conformable upwards passage from the Trigal Formation.

The lithology consists of a well-bedded sequence of sandstones, silicified shales, calcareous shales, coarse conglomerates, diatomites, and low-grade coals. The conglomerates are most common at the top and bottom of the formation. The sub-bituminous coal or lignite occurs in five principal seams in the Loja Basin, and in eight in the Malacatos

Basin. In the latter basin the coal seams are found in the lower part of the formation. The maximum thickness appears to 700 to 800 m.

Quillollaco Formation

The type locality is the stream (997, 502) 7 km south of Loja. The formation, which appears to succeed the San Cayetano Formation conformably in the Loja Basin, crops out on the west side of the basin. In the Malacatos Basin the contact with the San Cayetano is not seen, and the Quillollaco Formation rests unconformably on the older Tertiary formations.

The formation consists predominantly of coarse conglomerates with interbedded grits, greywackes, and sandstones. No fossils have been found in the formation. Kennerley (1973) thought that it was of Pliocene age; it is probably equivalent to the Santa Rosa Formation of the Cuenca Basin.

Flora, Fauna, and Age

Grebe (*in* Putzer, 1968:480), working on pollen, suggested a correlation between the coals of the Loja, Malacatos, and Cuenca basins.

The flora, unfortunately not stratigraphically located but probably from the San Cayetano Formation, was first studied by Engelhardt (1895) and subsequently by Berry (1918, 1929, 1934, 1945). Berry initially (1918) placed this tropical flora in the Lower Miocene, but in later revisions (1929, 1934, 1945) of this same flora, he regarded it as Mio-Pliocene, or Pliocene age. Some of these plants are known in the Nabón (Bristow, 1976) and Cuenca (Berry, 1934, 1945) basins.

Fish scales are common in the San Cayetano Formation, but the only fish so far identified, whose exact provenance is uncertain, is *Carrionellus dumorterei* White (1927).

The molluscs consist of *Dyris* cf. *gracilis* Conrad "form" *tricarinata* (Boettger) occurring on an unlocated slab sent to the British Museum of Natural History by Prof. Carrión, and in shales collected by the author and B. Kennerley from the San Cayetano Formation (JW424 [008, 582]). The latter are found as scattered impressions on the bedding surfaces of some of the shales.

D. gracilis tricarinata was described from Pebas, Peru (Boettger, 1878). It is also known from Iquitos, Peru (de Greve, 1938), Pichua near Cochiquinas, Peru (Hauxwell, Colln. BMNH), Canamá on Rio Javari, Peru (Etheridge, 1879 as *Melania bicarinata* nov. sp.), and in ?Pliocene beds at La Tagua, Ca-

queta River, Colombia (C. P. Nuttall, personal communication).

The Miocene ostracod *Cyprideis stephensoni* (Sandberg) has already been mentioned.

It is thus evident that the oldest non-volcanic deposits (Trigal Formation) is of Miocene age, as evidenced by *C. stephensoni*. The San Cayetano Formation, based on the similarity of its lithology and pollen to the Mangán Formation, is probably Upper Miocene.

DEPOSITS OF THE RIO PACHITEA AND VICINITY IN EASTERN PERU

The red beds of the Rio Pachitea area were mapped and discussed by Singewald (1927, 1928). Fossils collected during the field work were examined by Pilsbry (1944). Pilsbry made a comparison at generic level between the fauna from the Rio Pachitea and those from the Cuenca Basin, Ecuador, and from the Magdalena Valley, Colombia. At that time none of the species was known to occur in more than one of the three basins, though some of the [*Aylacostoma*] *Longiverena* are closely similar. Pilsbry concluded that until further collecting afforded a more definite clue to the age of the Pachitea deposits they could tentatively be considered to be about the age of the La Cira deposits—Upper Oligocene or Lower Miocene. Such differences as appeared between the faunas of the La Cira, Pachitea, and Cuenca beds were more likely to be due to their geographic separation than to any material difference in age. The correlation of these three deposits, and Pilsbry's age assignment of Upper Oligocene or Lower Miocene, based as it was on fairly slender evidence, has been corroborated by the present study. The common presence of *Pomacea mauco* in the Middle Miocene Loyola Formation of the Cuenca Basin and at Pachitea, suggests that the deposits at the latter locality might be slightly younger than thought previously. Koch and Blissenbach (1962:77), however, suggest that the Sol Formation, in which the fauna occurs, lies close to the Cretaceous/Tertiary boundary, or may be wholly Cretaceous (Koch and Blissenbach, 1962: fig. 21; pl. 3). The evidence for such a radical reassessment of the age is not convincing, being based on several new species of charophytes and new, unnamed, but numbered ostracods. Two species of charophytes (*Tectochara supraplana sulcata* and *Kosmogyrta monilifera*) from this area had earlier been considered as of Eocene or Oligocene age (Peck and Reker, 1947).

It is worth noting at this point that *Mitricaulis incarum* Pilsbry, described from "Marine [?Eocene] Tertiary of the Pachitea River," is now known from Maestrichtian sediments of the Cuenca Basin (R. Cleavelly determination in Bristow and Hoffstetter, 1977:351). The deposits with *M. incarum* underlie the non-marine fossils mentioned above; a Cretaceous age is not inconsistent for this part of the sequence.

MAGDALENA EMBAYMENT, COLOMBIA

Fossiliferous strata have been found at three principal levels in the Tertiary sediments of the Magdalena Valley between the Sogamoso and Carare rivers (Wheeler, 1935). As with Tertiary non-marine sediments elsewhere the fauna when described was entirely new and thought to be endemic. No independent dating of the associated strata was possible and only tentative ages could be assigned to the respective formations. However, some of the arguments for the age determination are in part circular as having "fixed" the age of the oldest, Los Corros, fauna at the top of the Esmeraldas Formation as Upper Eocene, the succeeding formations were tied into this chronology. Nevertheless, the various ages have never been seriously questioned and are generally accepted at the present day.

Esmeraldas Formation

Pilsbry and Olsson (1935:7) "based partly on stratigraphy and partly on faunal evidence" concluded that the Los Corros fauna belonged to the Upper Eocene, equivalent to the Saman Formation of Peru and the Jacksonian of the southern United States. The faunal evidence was based on the somewhat suspect comparison of two species of *Diplocyma* in the Los Corros fauna with one species, *Potamides lagunitensis* (Woods), in the Saman Formation. The overall fauna had an "Eocene rather than an Oligocene aspect." The stratigraphic evidence appears to be based on the fact that marine Upper Eocene rocks are widespread in the coastal region of Colombia and that therefore "it seems reasonable to believe that the non-marine equivalent of these rocks should occur in the Tertiary embayments, as well exemplified by the deposits of the Magdalena valley."

More recently Van der Hammen (1957:65), based on palynology, suggested an Upper Eocene date for the Esmeraldas Formation. However, the evidence is inconclusive because the pollen spectrum for the

Table 2.—Distribution of the non-endemic, Tertiary non-marine Ecuadorian Mollusca. Plus sign indicates species is present.

Species	Ecuador																Peru			Colombia					Vene- zuela	Brazil	Florida																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																							
	Cuenca					Loja	Río			Esme- raldas	Mugrosa	La		Real	Caqueta																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																			
	Chota	Loyola	Azogues	Mangán	Pachitea		Pebas	Canamá	Cira																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																									
<i>Diplodon (E.) guarani- anus bibbianus</i>		+																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																</

Upper Eocene is matched almost exactly by one in the Upper Oligocene (Van der Hammen, 1957: pl. 1). Additionally, the age of the Esmeraldas Formation to which the 'Upper Eocene' pollen zones correspond is regarded unequivocally as Upper Eocene because of the fossiliferous Upper Eocene horizon [Los Corros] which is contained therein. The circular argument for the age of this fauna is thus nearly complete. Germeraad et al. (1968: Fig. 17) have indicated that the base of the Esmeraldas Formation is of Middle-Upper Eocene age, but unfortunately the top of the formation in which Los Corros fauna occurs, has not been palynologically dated. The upper Eocene age of the Los Corros Formation is not established with any degree of certainty. The available evidence from Colombia (see Mugrosa below) does not preclude an Oligocene age for the fauna.

Mugrosa Formation

The Mugrosa Formation succeeds the Esmeraldas Formation with apparent conformity. The Mugrosa fossiliferous horizon varies from 360 to 1,350 m above the base. One species, *Aylacostoma eucosmius* (Pilsbry and Olsson), is also known from La Cira Formation, while the new species *Paleoanculosa kenneleyi* in the Upper Miocene Mangán Formation of the Cuenca Basin, previously indicated by Bristow and Hoffstetter (1977) as *A. sigma-chilus* (Pilsbry and Olsson) from the Mugrosa Formation, is very similar to the latter species.

Pilsbry and Olsson (1935:8) thought that some of the "Hemisinus" in the Mugrosa Formation were

closely related to forms known in the Middle Oligocene of Cuba and Antigua. At the time these authors were writing (1935), the Oligocene included the Aquitanian and Burdigalian stages which at the present day are considered as the lowest stages of the Miocene.

Hoffstetter (1970), however, suggests that these Cuban and Antiguan occurrences are of Lower Oligocene age. Van der Hammen (1960), without giving details, dated the lower part of the formation on pollen as Lower Oligocene, and the upper part as Middle Oligocene.

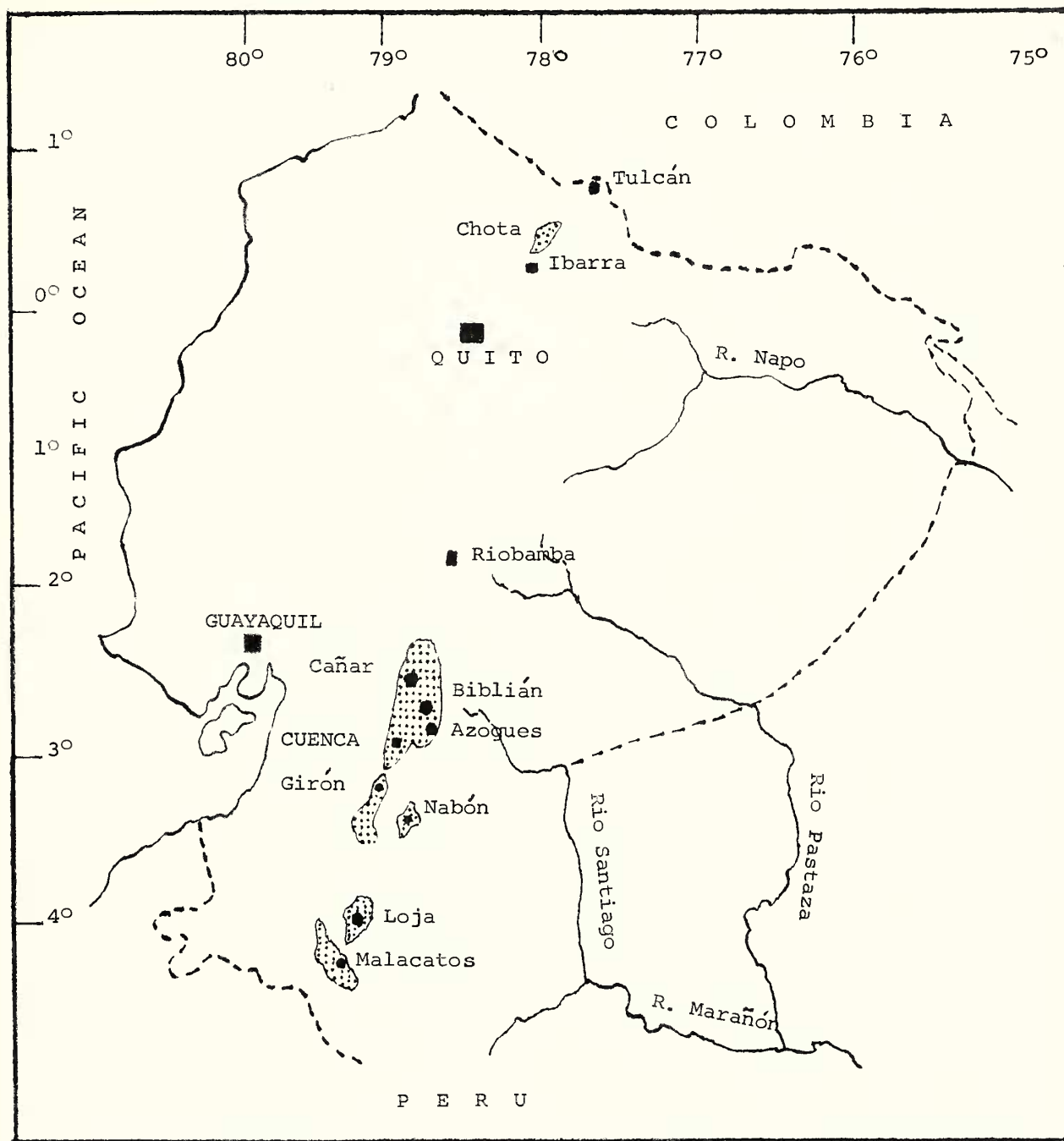
There appears to be a general agreement for the Oligocene age of the formation, but there is uncertainty as to whether it is of Lower or Upper Oligocene. Upper Oligocene is preferred.

La Cira Formation

This formation rests conformably on the Mugrosa Formation. The La Cira fossil horizon occurs some 780 to 2,070 m above the base of the formation. To date, only one of the molluscan species, *A. eucosmius* (= "Hemisinus" [Longiverena] laciranius Pilsbry and Olsson, 1935) is known outside this horizon in the Mugrosa Formation.

Wheeler thought that the fauna might be Upper Oligocene or Lower Miocene in age. Porta (1974), in a resumé of the age of the formation, suggested that the lower part was probably of Oligocene age, and the upper part of Miocene age.

The author favors a Miocene age for the La Cira fauna and, if the correlation first suggested by Pilsbry (1944) with the Cuenca and Pachitea deposits



Map 1.—Tertiary non-marine deposits of the Andes in Ecuador.

is substantiated, it may well be of Middle Miocene age.

CAQUETA BASIN, COLOMBIA

A recently described section (M. Eden, personal communication) along part of the Rio Caqueta in

southern Colombia has revealed fossiliferous strata of possible Pliocene age. These have been named the La Tagua Beds. They consist of up to at least 25 m of clay, silt, claystone, and siltstone, locally with sandy intercalations, and rest on the Upper Cretaceous Roraima Formation.

The molluscs from the La Tagua Beds have been

identified by C. P. Nuttall (personal communication). The fauna includes *Doryssa* sp., *Cochliopina* sp., *Aylacostoma browni* (Etheridge), *Hydrobia* cf. *ortoni* (Conrad), *Dyris gracilis* (Boettger), *Anisothyris erectus* Conrad, *Anisothyris* sp., and unidentifiable unionids. This freshwater fauna has close affinities with that from Pebas and Iquitos (only the *Doryssa* and *Cochliopina* are not known to occur at Iquitos and Pebas), and has a modern aspect. Nuttall concluded that the La Tagua Beds were late Cenozoic, possibly of Pliocene age. *A. browni* is known also from both the Middle and Upper Miocene Loyola and Mangán formations of the Cuenca Basin.

One described species of ostracod, *Pelocypris zilchi* Triebel, has been recorded from the La Tagua Beds (Sheppard and Bates, 1980). *P. zilchi* is known only from San Salvador where it occurs in strata of probable Pleistocene age (Triebel, 1953). Other new species and genera of ostracods are common to both the La Tagua and Pebas beds.

CANAMA, PERU

Brown (1879), who described the section at Canamá, and at several other localities downstream, distinguished an upper unit of younger (?Pleistocene + ?Holocene) river deposits, from the underlying, gently dipping, Tertiary rocks, of which a maximum of 20 m was seen at any one locality.

One fossil (*Aylacostoma browni*) from Canamá occurs in the Middle Miocene Loyola Formation and in the Upper Miocene Mangán Formation of the Cuenca Basin. It also occurs in the Pebas Beds. Other fossils from Canamá suggesting a good correlation with the Pebas Beds of Pebas, Pichua and Iquitos include *Pachydon carinata* Conrad, *P. tenuis* Gabb (= *hauxwelli* Woodward), *P. erectus* Conrad (= *tumida* Etheridge), *P. cuneatus* (Conrad) (= *Corbula canamaensis* Etheridge). Former authors used *Pachydon* as an alternate for *Anisothyris*.

IQUITOS AND PEBAS, PERU

Widespread fossiliferous strata have been found around Iquitos (see de Greve, 1938:13–18), at Pebas, some 30 mi below Pebas (Conrad, 1871), and at Canamá on the Rio Javary (Brown, 1879). Similar strata, but unfossiliferous, were noted by Brown (1879:76) at São Paulo, lower down the Amazon. The Iquitos and Pebas faunas have much in common and may be treated as one. They are also sim-

ilar to the deposits and fauna from Canamá which are described separately in this account.

Although widely distributed, the thickness of the fossiliferous strata and associated beds exposed at any one locality is not very much. De Greve (1938:16) described a partial 6.8 m section of blue and yellow clay which was observed in the Rio Itayá near Iquitos. Lignite is locally associated with the fossiliferous beds.

Some 42 fossils, dominantly molluscs, have been recorded from Pebas and it is the richest locality discussed in that paper. The fauna, both in numbers of species in common and in the method of preservation (as undistorted shells, commonly with the nacreous layer intact, and from which the matrix can be easily removed), is most closely linked to that of the La Tagua and Canamá localities where, to date, more limited faunas have been obtained. Two species (*Aylacostoma browni* and *A. sulcata*) are common to the Cuenca deposits and to the collective Pebas/La Tagua/Canamá faunas. Of particular interest is *A. browni*, as it is known in both the Loyola and Mangán formations of the Cuenca Basin, from La Tagua, from Canamá, and from Tres Unidos, Brazil (Parodiz, 1969:141 under the name *sulcatus*) and is thus the most widely distributed of the Tertiary non-marine molluscs in the area under discussion. However, *Anisothyris*, which is an important element of the Pebas and La Tagua faunas, is absent in the Cuenca Basin, but replaced by *Erodona*.

There is no independent method of dating this fauna. Most workers are agreed that it is of Tertiary age, although some deposits in nearby Brazil of similar lithology to that at Pebas and Iquitos have been shown to be Pleistocene (Simpson, 1961). The shell preservation (see above) presents a "young" aspect, and the fact that some shells retain their coloring has been cited as an indication of no great antiquity (Gabb, 1869:197). The difference in the method of preservation between the Amazonian faunas and those of the Andes may be no more than a reflection of the differing tectonic environments in which the deposits occur. Those of the Cuenca area, for instance, are strongly folded and faulted and have been uplifted by some 2,500 m (that is, from near sea level, as witnessed by *Necroneustes proavitus*) since deposition. Marine shells similarly preserved to those from Pebas are known from the Upper Miocene/Lower Pliocene deposits of coastal Ecuador (see for example, Pilsbry and Olsson, 1941). The retention of shell color cannot be taken

as an indicator of age because several of the *Neritina* in the Cuenca Basin still retain their markings, and the author has seen marine gastropods of Upper Miocene age from coastal Ecuador with their color preserved. Color pattern in the Neritacea is known from the Devonian onwards.

The common occurrence of four species from Cuenca and the Amazon clearly indicates no significant time gap between the respective faunas. In the author's opinion the Pebas fauna is probably of Upper Miocene or Lower Pliocene age.

SUMMARY OF OCCURRENCES IN CUENCA BASIN

Twenty-nine species of molluscs are now known from the Cuenca Basin, and one each from the Cho-

ta and Loja basins. Of this fauna, 12 species have been recorded outside Ecuador, principally from localities in the western Amazon Basin, suggesting that in earlier times, before the main Andean uplift, there was a closer connection between the Cuenca Basin (the present day Atlantic/Pacific watershed crosses the basin) and the western Amazonian deposits. The maximum age for the Cuenca fossils is uppermost Lower Miocene. It is suggested that other occurrences of the Cuenca fauna outside Ecuador might also be of Miocene age. The distribution of the non-endemic Cuenca molluscs outside Ecuador is shown in Table 2.

PART 2. PALEONTOLOGY

J. J. PARODIZ

INTRODUCTION

The majority of the Mollusca of the Tertiary, non-marine deposits of Ecuador belong to the upper section of the Lower Miocene, Loyola Formation, with brackishwater gastropods as *Neritina*, or purely freshwater bivalves of the Mutelacea and Unionacea. In the later, the Hyriidae in South America are known in South America since the early Paleocene in Patagonia.

Although fewer species are known from the Middle Miocene, Azogues Formation, and the Upper Miocene, Mangán Formation, such genera as *Neocorbicula* are common to both and found abundantly in all the Miocene. The freshwater cerithiaceans, *Aylacostoma*, *Doryssa*, and *Paleoanculosa*, are also abundant in the Mangán Formation and in the last genus, *P. kenneryleyi* is found in great numbers and is a characteristic of that formation. In the northern Chota Basin, the middle section contains exclusively the lacustrine *Liris minuscula*. In the Cayetano Formation in the Loja Basin (most probably Upper Miocene in age), the common species is *Dyris gracilis*.

The Miocene non-marine fauna of Ecuador dif-

fers, as a whole, from that known in Peru at Pebas and Iquitos, which is younger. In the Peruvian Pliocene, the large freshwater mussels of the Unionacea and Mutelacea are practically absent, but characterized by more species of *Neritina* and *Anisothyris*. *Anisothyris* is not found in the Ecuadorean Miocene but replaced by *Erodona*, although it is not common. Also the *Neocorbicula* and *Paleoanculosa* are absent in the Peruvian Pliocene. The present knowledge of the Miocene malacofauna of Ecuador permits the reconsideration of the age of Pebas—not only have some Pebas species been found in Cuenca, Loja, and Chota basins, but also very few of the known species from Pebas have survived. Pebas is, probably, not younger than the Lower Pliocene.

Table 3 includes all the species known from the Ecuadorean Miocene. Only one species is confirmed as surviving in the Recent fauna, but as an allochronic subspecies—*Diplodon (Ecuadorea) guaranianus guaranianus*. The *Ostomya* that is listed here as *O. "cfr." fluviatilis* has affinities with this living species, although it may not be the same.

SYSTEMATIC ACCOUNTS

Class Bivalvia

Superfamily Unionacea

Family Hyriidae Swainson, 1840
(Ortmann's Hyriinae of "Mutelacea")

Subfamily Hyriinae, restricted

Parodiz and Bonetto, 1965

Tribe Diplodontini (Diplodontidae Ihering, 1901)

Genus *Diplodon* Spix, 1827

Iridea Swainson, 1840.

Prodiplodon Marshall, 1928.

Eudiplodon Marshall, 1928.

Schleschiella Modell, 1950.

Type species.—*Diplodon ellipticus* Spix (in Wagner, 1827), on pl. 16, figs. 1–2.

Adams and Adams (1854) under the name *Diplodon* included an heterogeneous conglomeration of species from all over the world. The genus was geo-

graphically restricted to South America by Ortmann (1921); the variable characteristics of the shells have recurrent features among the species groups and subgenera.

Ortmann was the first to study the glochidia of many species, but he did not use those embryological features for subgeneric divisions. Accepting Simpson's two subgenera, *Diplodon* sensu stricto and *Cyclomya* (now under the correct name *Rhipidodonta*), Ortmann recognized within the first a group of species around *Diplodon hylaeus*, which subsequent authors included in *Ecuadorea* Marshall and Bowles. When the condition of the larval stages became better known, the main groups were separated on that biological basis. According to Bonetto (1965a and after), most of the better known species belong to two groups: 1) with parasitic glochidian larvae; shells are usually longer than high;

Table 3.—*Species of Mollusca known from the Miocene of Ecuador. A plus sign indicates that the species is known from the basin.*

Species	Chota Basin	Cuenca Basin			Loja Basin
		Loyola Formation	Azogues Formation	Mangan Formation	
Bivalvia					
Superfamily Unionacea					
Family Hyriidae					
<i>Diplodon (Ecuadorea) guaranianus biblianus</i> (Marshall and Bowles)		+			
<i>Diplodon (E.) bristowi</i> , new species		+			
<i>Diplodon (E.) liddlei</i> (Palmer)		+			
Superfamily Mutelacea					
Family Mycetopodidae					
Subfamily Monocondylaeinae					
<i>Fossula derbyi</i> (Ihering)				+	
<i>Monocondylaea azoguensis</i> (Palmer)		+			
<i>Monocondylaea pacchiana</i> (Palmer)		+			
<i>Monocondylaea</i> sp.		+			
Subfamily Anodontitinae					
<i>Anodontites olssoni</i> (Palmer)		+			
Superfamily Sphaeriacea					
Family Sphaeriidae					
<i>Pisidium</i> sp.		+			
Family Corbiculidae					
<i>Neocorbicula cojitamboensis</i> (Palmer)		+	+	+	
Superfamily Myacea					
Family Corbulidae					
<i>Erodona iquitensis</i> (de Greve)		+			
<i>Ostomya</i> cf. <i>fluviatilis</i> (H. Adams)		+			
Gastropoda					
Superfamily Trochacea					
Family Trochidae					
? <i>Caliostoma</i> sp.		+			
Superfamily Neritacea					
Family Neritidae					
Subfamily Neritinae					
<i>Neritina pacchiana</i> Palmer		+		+	
<i>Neritina loyolaensis</i> , new species		+			
<i>Puperita</i> aff. <i>sphaerica</i> (Olsson and Harbison)		+			
Superfamily Cyclophoracea					
Family Aperostomatidae					
<i>Poteria (Pseudoaperastoma) bibliana</i> (Marshall and Bowles)		+			
Superfamily Viviparacea					
Family Ampullariidae					
<i>Pomacea (Limnopomus) manco</i> Pilsbry		+			
Superfamily Rissoacea					
Family Hydrobiidae					
<i>Hydrobia ortonii</i> (Gabb)		+			
<i>Liris minuscula</i> (Gabb)	+				
<i>Dyris gracilis</i> Conrad					+
<i>Lyrodes</i> sp.		+			
<i>Toxosoma eboreum</i> Conrad				+	
<i>Potamolithoides biblianus</i> Marshall and Bowles		+			

Table 3.—Continued.

Species	Chota Basin	Cuenca Basin			Loja Basin
		Loyola Formation	Azogues Formation	Mangán Formation	
Superfamily Cerithiacea					
Family Thiaridae					
<i>Aylacostoma sulcatus</i> (Conrad)				+	
<i>Aylacostoma browni</i> (Etheridge)		+		+	
<i>Aylacostoma</i> sp.			+	+	
<i>Aylacostoma dickersoni</i> (Palmer)		+	+		
Family Pleuroceridae					
<i>Doryssa bibliana</i> (Marshall and Bowles)		+		+	
<i>Paleoanculosa kennerleyi</i> , new species				+	
Superfamily Lymnaeacea					
Family Planorbidae					
<i>Gyraulus</i> sp.		+			
Superfamily Succineacea					
Family Succineidae					
<i>Succinea</i> sp.		+			
Incertae sedis		+			

subgenus *Diplodon* s.s.; 2) with glochidia of direct development; shells with greater height about the middle of the valve, subrotund; subgenus *Rhipidodonta* Mörch, 1853 (= *Cyclomya*).

Although the glochidial development is still unknown in a good number of species, and shell variation is considerable, the system is workable for the main group of species. One of these groups, with shells like those in the first group (to which the Miocene Ecuadorean species belong), have non-parasitic glochidia as *Rhipidodonta*; also they present reduction in size, and greater development of umbonal sculpture forming radial V's inserted one into the next, reaching the center of the disc or, occasionally, the ventral margin. These were included by Modell (1950) in the genus *Ecuadorea*. The oldest of this group were found in the Oligocene of Peru, and several are still living in the northwest, middle, and southwest of South America, but absent in eastern Brazil. Shell characteristics in this group seem to be more constant than those found between the subgenera *Rhipidodonta* and *Diplodon* s.s.

The parasitic glochidia are probably a more primitive type, and non-parasitic glochidia are a secondary evolutionary development; this is suggested by the oldest forms of *Diplodon* in the Paleocene, while *Ecuadorea* appears later in the Tertiary (a similar parallel evolution occurred also in other Unionacea families of North America). T. R. Roberts (1975) described remains of fossil fish of the genus *Hoplias* in the Ecuadorian Miocene; parasitic

glochidia have been found with frequency in the fish *Hoplias malabaricus* of the Paraná, producing cysts in the gills. If the fossil *Ecuadorea* had a transitional type of glochidia with any relationship with the fossil *Hoplias*, it could not be verified; however, their direct descendant living species in *Ecuadorea* have all non-parasitic glochidia.

The distinction between the flat and elongated *Diplodon* s.s. and the short, inflated and strongly costulated *Ecuadorea* is already evident in the Paleocene species; the *Diplodon* are extraordinarily similar to their ancestors from the Triassic of Pennsylvania. Pilsbry (1921) described several species of that age from York Co., Pennsylvania, which he stated are "like *Diplodon* and *Hyria* and totally unlike that of *Unio* and allied genera of the Northern Hemisphere." Comparison of *Diplodon pennsylvanicus* Pilsbry from the Triassic with *Diplodon bondembenderi* Doello-Jurado from the Paleocene of Patagonia shows that they belong to the same group. Richards (1948) also described *Antediplodon borealis* (using Marshall's generic name) from the Newark series of York Co., which has a shape similar to that of the living *D. rhuacoicus* group.

A full generic separation of *Ecuadorea* from *Diplodon*, however, would obscure rather than clarify taxonomic relationship. Obviously Modell (1950) was not entirely acquainted with all the fossil and living species involved. For practical purposes, *Ecuadorea* can be accepted as a subgenus. In order to avoid repetitious comments when describing the

fossil species from Ecuador, it is pertinent here, to give a brief account of the other species that can be assigned to *Ecuadorea*.

Diplodon latouri (Pilsbry and Olsson, 1935).—Oligo-Miocene of La Cira Formation, Colombia (see Parodiz, 1969:62). Described as *Triplodon*, it is the oldest species of the group and also the smallest (known only by the type, it might be a juvenile). The V-shaped sculpture reaches only—as in *guaranianus bibliauus*—the middle of the disc. The authors already indicated that it may be referred to *Ecuadorea*.

Diplodon (Ecuadorea) hylaeus (d'Orbigny, 1842).—Type locality: Palometas River, north-central Bolivia (specimens usually labelled as *D. hylaeus* from southeastern localities actually belong to *D. guaranianus*). It is very rare, as its author remarked. Extremely thin compared to *D. guaranianus*, so much that the external ribs can be seen strongly marked on the internal surface which is very iridescent instead of white, and hinge and muscle scars weaker.

Diplodon (Ecuadorea) hylaeus pazi (Hidalgo, 1868).—Described originally as *Castalia*. Type locality: Imbabura, Ecuador. Differs from *D. hylaeus* by its sculpture reaching the ventral margin very regularly. It is a living subspecies.

Diplodon (Ecuadorea) guaranianus (d'Orbigny, 1835).—Described originally as *Unio*. Type locality: Paraná River at Itaty, Corrientes, Argentina. The most abundant living species, showing clinal variation in its distribution along the Paraná-Paraguay drainage. *D. asuncionis* Marshall from Paraguay, and *D. hasemani* Ortmann from the Guaporé River, Brazil, correspond to such clinal forms. This species has a very strong and heavy shell, as well as a strongly developed hinge, and the interior of the valves is pure white.

Diplodon from the Miocene of Ecuador

Subgenus *Ecuadorea* Marshall, 1934

Castalioides Marshall, 1934.

Type species.—*Ecuadorea bibliana* Marshall and Bowles.

Original description.—"Hyriinae with plentiful radial sculpture similar to that of *Diplodon* and still more similar to that of *Hyria*. The radial ribs are arranged in V pattern, each V nesting in a succeeding one. Posterior dorsal area with several plicae crossing it obliquely to the margin."

Original description of *Castalioides*.—"Shell with strong sculpture of radial ribs, several of the innermost pairs arranged

to form very long Vs. Ribs crossing the anterior and posterior slopes form a divaricate pattern with the radial ribs."

Type.—*C. laddi*, "Quaternary," Venezuela.

These two diagnoses, although differently worded, say the same thing. *Castalioides* cannot be separated from *Ecuadorea*. The authors of *Ecuadorea* said that "it is difficult to decide the relationship of this genus to Recent genera . . . in form the shell is like *Diplodon* but that genus is not plentifully sculptured." The similarities of *Castalioides laddi* are of the same order as those found in *Diplodon guaranianus* in relation to *D. bibliauus*. Marshall and Bowles also found resemblances of *Ecuadorea bibliana* with "*Castalia*" *pazi* Hidalgo, which now is recognized as a *Diplodon*. The hinge of *Castalioides*, which in Palmer's (Liddle and Palmer, 1941) opinion is apparently different from that of *Ecuadorea*, does not differ from some of the variations present in the living *D. guaranianus*.

Diplodon (Ecuadorea) guaranianus bibliauus (Marshall and Bowles)

Ecuadorea bibliana Marshall and Bowles, 1932:5, figs. 7–8;

Palmer, 1941:401, pl. 7, figs. 1–6.

Castalioides laddi Marshall, 1934:78, figs. 1–4; Palmer, 1941:402.

Ecuadorea laddi, Modell, 1950:143.

Diplodon guaranianus bibliauus, Parodiz, 1969:66, pl. 6, figs. 1–7, pl. 8, fig. 6; Bristow and Hoffstetter, 1977:183.

Type locality.—Biblián, northwest of Azogues, Loyola Formation, Ecuador. Type in NMNH.

Specimens observed.—Localities CRB 18 and 28 (sandstones and conglomerates), Basal Loyola Formation NW of Loyola.

Original description.—"Shell rather compressed, slightly narrower in front. Concentric sculpture of fine growth striae, with a few of the rest periods a little accentuated. Radial sculpture of a number of riblets as to form a series of V's, and with other riblets at the front and back which if continued would form additional V's. The anterior prong of each V is narrow, clear-cut, and nearly straight. The posterior prong is heavier and more irregular and curves toward the front of the shell. At the lower end where the radial sculpture dies out, the surface is somewhat pimpled. The posterior dorsal area with several (five or six) distinct flutings running across it to the margin. The dorsal and ventral margins both arquate. L. approx. 33 mm, H. 24 mm (half 11 mm)."

Remarks.—Complete discussion of this subspecies is found in Palmer (Liddle and Palmer, 1941) and Parodiz (1969). Palmer suggested that the sculptural pattern of *E. bibliauus* has similarities with *Diplodon santamariae* Simpson, but this species (type in NMNH) has only one small V at the umbo, the rest being short and corrugated, and

its position is within the group of *Diplodon delodontus* (Lam.) with parasitic glochidia (see Parodiz, 1973:264). Its distribution is in southern Brazil.

The specimens observed from Basal Loyola (CRB 18) are higher, in relation to the length if compared with the dimensions given for the type. The half diameter of these specimens remains the same, appearing flatter, and thus differing from the typical *D. guaranianus guaranianus*, which is always inflated and stronger.

Diplodon (Ecuadorea) bristowi, new species

Holotype.—British Museum LL27820 is in a matrix from locality CRB 18b of Basal Loyola Formation (Lat. 2°43'20"S, Long. 78°51'45"W) in same deposit containing *Monocondylaea azoguensis* and from an altitude of 2,530 meters.

Description.—Valve (right) relatively small. Umbo well advanced toward the anterior margin. Shape triangular-oval; the anterior half of the valve is perfectly round, while the posterior is decidedly triangular, more so than in other congeneric species, especially at the posterior lower margin; thus, the slope of the dorsal margin falls very obliquely. Sculpture consisting of 30 radial ribs, not chevroned but irregular on the umbonal area, and becoming increasingly wider toward the lower margin and especially on the posterior side. The ribs closer to the anterior margin are almost vertical, becoming more oblique in proportion as they approach the posterior margin, then following the direction of the slope, where they are also thicker and more separated. Without coarse lines of growth but, instead, being concentrically striated with very fine incisions crossing the ribs as well as the interspaces (5 or 6 of such incisions can be counted per mm). Length 25 mm, height 19 mm. Anterior rounded side less than half of the triangular posterior.

Comparisons.—The peculiar triangular shape acutely angulated on the posterior side, its regularly rounded anterior portion, the absence of coarse concentric lines on the lower part of the valve, and its sculpture distinguishes this new species from *D. biblianus*. Compared with Recent species, *D. (E.) bristowi* appears as an ancestor of *D. (E.) pazi* from northwestern Ecuador, which has a similar type of radial sculpture, but differs in the other described features.

Diplodon (Ecuadorea) liddlei (Palmer)

Diplodon liddlei Palmer, in Liddle and Palmer, 1941:404, pl. 8, figs. 1–5; Parodiz 1969:66, pl. 8, figs. 1–4; Bristow and Hoffstetter, 1977:183.

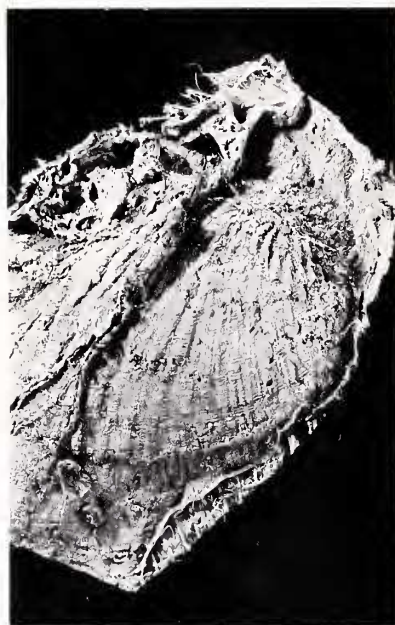


Fig. 1 (top).—*Diplodon (Ecuadorea) guaranianus biblianus* (BM LL27807). From Loyola Formation. $\times 2$.

Fig. 2 (bottom).—*Diplodon (E.) bristowi*, new species (BM LL27820). From Loyola Formation. $\times 2$.

Type locality.—Center of Azogues anticline, northwest of Azogues, Cañar, Ecuador. Type in Paleontological Research Institute, Ithaca, New York.

Specimens observed.—Loc. CRB 7, Biblián sandstones and conglomerates (Basal Loyola Formation NW of Loyola).

Original description.—"Shell elongate-quadrate, plump, anterior end short flaring dorsally with a narrow wing above the hinge line; posterior dorsal area concave; sloping ventrally; hinge with two pseudocardinals in the right valve, the lower tooth larger, with a large socket between; correspondingly a large pseudocardinal in the left valve; anterior adductor and re-



Fig. 3 (left).—*Fossula derbyi* (BM LL27806). Mangán Formation. Natural size.



Fig. 4 (right).—*Monocondylaea azoguensis* (BM LL27813). Basal Loyola Formation. Natural size.

tractor muscle scars preserved in paratype; umbones ornamented with radial ribs of short interlocking V-shaped pattern. The lower portion of the shell is sculptured with coarse lines of growth only. L. 35 mm, H. 28 mm, semidiameter 6 mm."

Remarks.—The shell is approximately of the same size as *D. (E.) bibbianus* but more compressed and with stronger hinge. The ornamentation scarcely reaches the center of the disc. The ornamentation scarcely reaches the center of the disc. Although Palmer assumed that *liddlei* has similarities in the hinge and other shell characters with *Diplodon mogymirim* Ortmann. *D. mogymirim* is a southeastern form from São Paulo, Brazil, with parasitic glochidia, and is a synonym of *D. expansus* (Kuster) (see Parodiz, 1973).

Superfamily Mutelacea

Family Mycetopodidae Gray, 1840

(restricted Conrad 1853)

Subfamily Monocondylaeinae Modell, 1942

Tribe Fossulini Bonetto, 1966

Genus *Fossula* Lea, 1870

Fossicula Marshall, 1925, an error.

Type species.—*Monocondylaea fossiculifera* d'Orbigny, 1835. Subseq. designation by Ihering, 1893. =*Fossula balzani* Ihering, 1893.

The main character in this genus is the double pseudocardinal in the right valve, instead of a single

tooth as in *Monocondylaea*, and the teeth are stumpy, not spatuliform, with a narrow and sinuous hinge plate bearing tooth-like irregularities on the posterior side. The umbonal cavity is not so deep as in *Monocondylaea* and the anterior adductor is shallower. *Fossula* probably represents a primitive type in the subfamily.

Fossula cf. *derbyi* (Ihering)

Fig. 3

Diplodon derbyi Ihering, 1907:466, pl. 18, fig. 128; Parodiz, 1969:82, pl. 8, fig. 3.

Remarks.—The one internal cast available from Loc. CRB 36b, Mangán Formation, Upper Miocene of the Cuenca Basin, is not well preserved. Its determination as *F. derbyi* is only tentative by comparison with the incomplete type of the species from strata of uncertain age (probably Upper Tertiary) in Rio Grande do Sul, Brazil (see Parodiz, 1969). Most of the living and fossil *Fossula* are known from southern South America, and only one species, *F. venezuelensis* Pilsbry and Olsson, is known from north of the Amazon. It must be added that the very brief description of "*Diplodon*" *derbyi* does not conform with the figured type. New discoveries are needed either in Ecuador or Brazil, to clarify the position of these fossils. The specimen is in British Museum, LL27806.



Fig. 5.—*Monocondylaea* sp. (BM LL27813a). Basal Loyola Formation. Natural size.

Tribe Monocondylaeini

Characterized by a well developed tuberculiform or spatuliform pseudocardinal, sometimes folded in the appearance of a double one.

Genus *Monocondylaea* d'Orbigny, 1835

Aplodon Spix, 1827 (not *Aplodon* Rafinesque, 1818, a *nomen nudum* in Pulmonata¹).

Spixiconcha Pilsbry, 1893, substitute for *Aplodon*.

Type species.—*M. paraguayana* d'Orbigny, 1835.

Remarks.—This genus is, according to Bonetto (1966), not a primitive one but a more specialized one among the South American Mutelacea, and it is widely distributed. Although the hinges of the fossil species described are mostly unknown, the genus can be recognized by its rather solid, subquadrate shell, without radial sculpture; the cloth-like periostracum characteristic of the living species is, of course not observable. The prismatic

area is wide and rather thick, and the valves sometimes gaping. The oldest species known is *Monocondylaea marshalliana* Pilsbry, 1935, from the Oligocene of Colombia.

Monocondylaea azoguensis Palmer

Fig. 4

?*Monocondylaea azoguensis* Palmer, in Liddle and Palmer, 1941: 405, pl. 9, fig. 8; Parodiz, 1969:78, pl. 8, fig. 5; Bristow and Hoffstetter, 1977:183.

Type locality.—Biblián sandstone, 3 km NW Azogues, Ecuador (Basal Loyola Formation). Holotype (a cast) in Paleontological Research Institute, Ithaca, New York.

Material examined.—One specimen, Brit. Mus. Nat. Hist. (LL27813) coll. CRB 18b.

Original description.—"Shell quadrate, short, anterior and ventral margins rounded; dorsal margin high; posterior margin obliquely inclined to about the middle line, then it turns and is broadly rounded to the ventral margin. An obscure fold occurs from the umbonal area to the point of angulation of the mid-posterior junction. It resembles the posterior folds of *Monocondylaea*. A second line is suggested from the posterior-ventral junction toward the umbo but crushing in that area indicates that the mark is not normal. The shell [sic] is smooth with no impression of radial sculpture on the beak. The anterior portion is not produced just below the beak as in most *Monocondylaea*. The hinge is not available and the specimens are poorly preserved. L. 29 mm; H. 25 mm; semidiameter 5 mm (cast)."

Remarks.—The hinge has not been observed because of the condition of the fossil specimen. The species can be distinguished from *M. pacchiana* by being shorter and more quadrate; it is also about 25% smaller than *pacchiana*.

Monocondylaea pacchiana Palmer

?*Monocondylaea pacchiana* Palmer, in Liddle and Palmer, 1941: 49, pl. 9, figs. 1–2 (*pacchensis* in plate); Parodiz, 1969:80, pl. 8, figs. 2, 7; Bristow and Hoffstetter, 1977:183.

Type locality.—Biblián sandstone at Quebrada Paccha, Azuay, Ecuador (=Basal Loyola Formation). Syntypes at Paleontological Research Institute, Ithaca, New York.

Original description.—"Shell medium, umbos low, dorsal line straight; posterior end broad, straight or slightly rounded, anterior end sloping, short; shell smooth; hinge unknown. L. 40 mm; H. 33 mm; semidiameter 10 mm."

Remarks.—Described from fragments of the shell adhering to the cast. The concentric growth lines define it better than *azoguensis* as a *Monocondylaea* as does the absence of radial sculpture. It is possible that *pacchiana* represents a more mature form of *azoguensis*, because both belong to Basal

¹ The name *Aplodon* Rafinesque is a *nomen nudum* and therefore does not pre-occupy the name. Spix's name which was not in use for more than 50 years is according to the ICZN (article 23b) a *nomen oblitum*. Therefore the better known name of *Monocondylaea* is maintained.

Loyola; the differences in the currently known materials may be verified when better specimens become available.

Monocondylaea sp.

Fig. 5

Remarks.—The specimen consists of the lower half of an internal cast from locality CRB 18, Basal Loyola. The middle line of the posterior dorsal margin and inflation toward the center reveals it to be a *Monocondylaea* dissimilar to the above mentioned species, but the condition of the cast makes it insufficient for description. The specimen is British Museum, LL27813.

Subfamily Anodontitinae Modell, 1942

Genus *Anodontites* Bruguere, 1792

Patularia Swainson, 1840.

Glabaris Gray, 1847.

Styanodon Martens, 1900.

Pachyanodon Martens, 1900.

Ruganodontites Marshall, 1931.

Type species.—*Anodontites crispata* (Bruguere, 1792 (orig. design.))

This genus is distributed in all South America from Colombia to northern Patagonia, with exception of the Pacific slope from Ecuador southwards. Its edentulous, *Anodonta*-like hinge is characteristic, differing from *Leila* which has incipient crenulations or articulations and more anteriorly pointed valves. The shells are elongated in most species and not—or very slightly—gaping. In very gerontic anodontitinae, the hinge line may present saliences in one valve that correspond to sinuses in the other, but such condition does not constitute an articulate hinge. In most fossils, however, the hinge has not been observed. The larger and greener species without surface ornamentation differ somewhat from the typical group of *A. crispata*, and have been separated in *Glabaris*; however, because there are intermediate forms, the subgeneric divisions proposed are still very unsatisfactory. In Ecuador only a very rare species has been found living, *A. napoensis* (Lea), which Marshall (1931) included in his *Ruganodontites* and which according to Haas (1931) is a form of the common and variable *A. crispata*. However, the fossil species from Ecuador cannot be compared with those now living in the northern part of the continent, except in regard to the light radial sculpture preserved only on the lower part of the shell. The specimens are assigned to the following species:

Anodontites olssoni Palmer

Anodontites olssoni Palmer, 1941:406, pl. 9, figs. 6–7; Parodiz, 1969:86; Bristow and Hoffstetter, 1977:183.

Anodontites sp. Marshall and Bowles, 1932:6.

Type locality.—Biblián sandstone, west of Azogues.

Material examined.—From loc. CRB 18, Basal Loyola.

Original description.—“Shell large, thick, umbos large, swollen; hinge line straight [in the remarks the author said that the dorsal line is displaced]; posterior end slopes obliquely from the posterior termination of the hinge line to the rounded posterior-ventral margin. Hinge unknown; surface smooth with conspicuous, radiating, undulating lines over the anterior portion of the shell from about the middle to almost the anterior margin, stronger ventral; irregular stages of growth. L. 65 mm; H. 46 mm; thickness (both valves) 35 mm.”

Remarks.—A noticeable condition in this species is that in casts found with both valves together one valve slips under the other. Palmer as well as Marshall and Bowles remarked that “one valve has slipped toward the ventral margin so that the beak is beneath the beak of the other valve.” The species apparently forms a transition between *A. crispata* and those equally rounded and swollen species of the southern regions which do not have conspicuous ornamentation. An older species, *A. lacirianus* Pilsbry and Olsson from the Oligocene of Colombia, has a shape rather similar to *A. olssoni*, but its surface is smooth.

Superfamily Sphaeriacea

Family Corbiculidae (=Cyrenidae of authors)

Genus *Neocorbicula* Fischer, 1887

Cyanocyclus Ferussac, 1811 (in part of authors).

Type species.—*Tellina limosa* Maton (= *Cyclas variegata* d'Orbigny).

A typical Neotropical genus, with long siphons (these are about 10 mm long observed in live specimens), having the same crenulations on the lateral teeth, and concentric sculpture as the Old World *Corbicula*, but differs by the presence of a pallial sinus and in the development of the embryos.

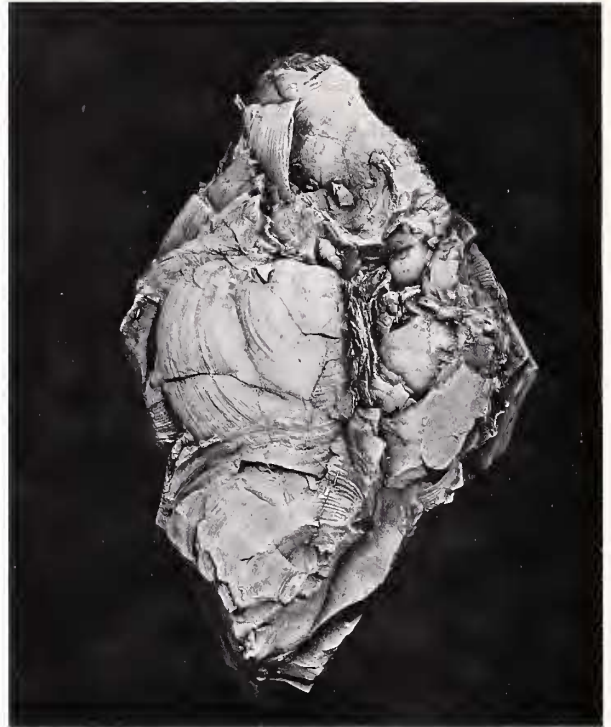
Neocorbicula cojitamboensis (Palmer)

Figs. 6–7

Corbicula (*Cyanocyclus*) *cojitamboensis* Palmer, 1941:408, pl. 9, fig. 6.

Corbicula (*C.*) *pacchiana* Palmer, 1941:407, pl. 9, fig. 5.

Neocorbicula cojitamboensis, Parodiz, 1969:92, pl. 10, fig. 11; Bristow and Hoffstetter, 1977:183, 194.



Figs. 6-7.—*Neocorbicula cojitamboensis* (BM 278331). Gray shale conglomerate from Mangán Formation. Natural size.

Neocorbicula pacchiana, Parodiz, 1969:91, pl. 10, fig. 1; Bristow and Hoffstetter, 1977:183.

Type locality.—Arroyo Potrero west of Cojitambo, near Cuenca, in bituminous limestone of Mid-Miocene (the deposit corresponds to Loyola Formation). Type in Paleontological Research Institute, Ithaca, New York.

Localities.—Middle Miocene: Basal Loyola, CRB 6, 7, 9, 10, 15, 18, 26, 34, 48; Middle Loyola, 11a, 11c; Upper Loyola, 11b; Basal Azogues, 1, 4, 13. Upper Miocene: Mangán, 20, 36, 42; Ayancay, 39.

Description.—Shell trigonal in shape; size as the average in living species. Umbo high; hinge with narrow laterals; surface with well marked concentric ribs and lines of growth. Height 19 mm (larger specimens 23), major diameter 21 mm (wider specimens 26), lesser diameter 4 mm when well preserved (most fossils are very compressed laterally).

Remarks.—The original descriptions of *cojitamboensis* and *pacchiana* are almost identical, except for the size indicated as larger in *pacchiana*. In her comments Palmer added that the “*Paccha Cyano-cyclas* differ in being less concave beneath the beaks”; this character is not very conspicuous in the fossils and it is highly variable in living species.

The uncertainty about the deposit in which *pacchiana* was found, in relation to the limestone with *cojitamboensis*, was the main criterion used to separate them as different species. The numerous samples collected by Bristow from the Lower to the Upper Miocene show all the intermediate variations as belonging to one and the same species. Those of localities 36 and 42 in the Mangán Formation are relatively larger but still not specifically separable. Most of the fossils, in the same shales containing *A. browni*, underwent a diatrophic process of compression in such a way that in many shells only the upper disc remains elevated, while the lower part down to the ventral margin is flattened. From matrices of Basal Loyola, the numerous casts in the yellowish sandstone are not well preserved, and are mostly fragments.

The name *pacchiana* takes precedence in Palmer's description being immediately above *cojitamboensis*; however, the type of *cojitamboensis* is a better preserved specimen, with more conspicuous characters. For this reason, and according to Article 24A and recommendation of the ICZN, *cojitamboensis* can hold priority.

Biological remarks.—Living *Neocorbicula* have

a brownish-green periostracum and the internal surface of the shell is tinted with violet. They are viviparous, whereas in the genus *Corbicula* there is a late larval benthic stage. Eggs of *Neocorbicula* are 5 mm in diameter; after hatching inside the internal marsupial gill the embryos are uncommonly long (some one-quarter the size of the maternal shell) and of an advanced stage of development, looking as exact miniatures of the adult. The individuals become sexually mature before they reach the average adult size, and in the marsupium of very small specimens (only one-third of the adult size) I found embryos 1.5 mm long. Larger embryos are located in the upper part of the gill and the smaller at the bottom of the marsupium. After dissecting more than a thousand individuals from different populations and localities (see Parodiz, 1965), no males were found and all individuals were gravid females. The embryos inside the same individual show an extraordinary resemblance to each other, but differ from individuals of other demes, thus forming not clines but clones. Such a characteristic points to parthenogenesis. The fossil shells of *Neocorbicula cojitamboensis* show that the same clonic condition existed in the Miocene.

Although most of the living *Neocorbicula* are found in river systems that empty into the Atlantic, they occurred abundantly during the Tertiary on the western part of the continent (*N. stelzneri* Parodiz in northwestern Argentina) and also in the Paleocene of Patagonia (*N. pehuenchensis* Doello-Jurado).

Family Sphaeriidae Jeffreys, 1862

(According to Article 40 of the ICZN Code, Sphaeriidae Jeffreys has priority over Sphaeriidae Erichson, 1845 in Insects.)

Cycladidae Rafinesque, 1820, *nomen oblitum*.

Pisidiidae Gray in Turton, 1857.

Genus *Pisidium* Pfeiffer, 1821

This genus differs from other Sphaeriidae by its inequilateral shell with the umbos not subcentral but towards the front.

?*Pisidium* sp.

Remarks.—The extremely small size (about 1 mm) of the ferruginous or blackish casts in a hard sandstone matrix made the assignation to *Pisidium* as only tentative. The matrix corresponds to the loc. CRB 7, of Basal Loyola and contains also remains of neritoid brackishwater snails, as well as Hydrobiidae and Planorbiidae, and also *Erodona*.

Other similar casts are found in loc. 26i. Roberts (1975:262) indicated ?*Pisidium* from CRB 11 (Middle Loyola) in deposits with numerous fragments of *Neocorbicula*. The deposits may represent a strand in which embayment brackishwater materials are mixed with drifted freshwater shells.

Superfamily Myacea

Family Corbulidae

Genus *Erodona* Daudin in Bosc, 1808

Potamomya Sowerby, 1839.

Azara d'Orbigny, 1839.

Type species.—*Erodona mactroides* Daudin, 1808 (= *Mya labiata* Maton, 1809).

Suter (1913) used *Corbula* (*Erodona*) for species from New Zealand which do not belong to this group. *E. mactroides* is found in the marginal brackishwaters of La Plata estuary and in similar locations in southern Brazil. "*Potamomya*" *ochreata* Hinds, usually indicated as a synonym, or possibly a subspecies, lives in the freshwaters of the Amazon. In Pleistocene deposits of the southern areas, *E. mactroides* is abundantly found. No fossil forms were recognized for the northern and northwestern part of the continent (in our present contents, from Ecuador). Authors dealing with this group of corbulids, Conrad, Dall, and de Greve, remarked on its relationship with the *Pachydon-Anisothyris* group. It is significant that Pilsbry and Olsson (1935), describing *Corbula magdalensis*, from the Miocene of Colombia, indicated *Erodona* as a possible subgenus. The history and taxonomy of *Erodona mactroides* has been thoroughly studied by Carcelles (1941) with photographs of the several individual variations.

?*Erodona iquitensis* (de Greve)

Fig. 8

Anisothyris iquitensis de Greve, 1938:46, pl. 5, figs. 38–41.

Remarks.—This species has more features that resemble *Erodona* than species of *Anisothyris*. It differs from *A. obliquus* Gabb (the accepted type of *Anisothyris*) and other species in the group, in that the shell is wider than high and the umbos are less tumid and not so strongly prosogyrate; the resilium and corresponding chondrophore are vertical, not oblique or almost horizontal as in *Anisothyris*, and lacks the stumpy, mamillaeform cardinal-like tooth; the tooth, divided, is the same, but proportionally smaller, as in *Erodona*. The

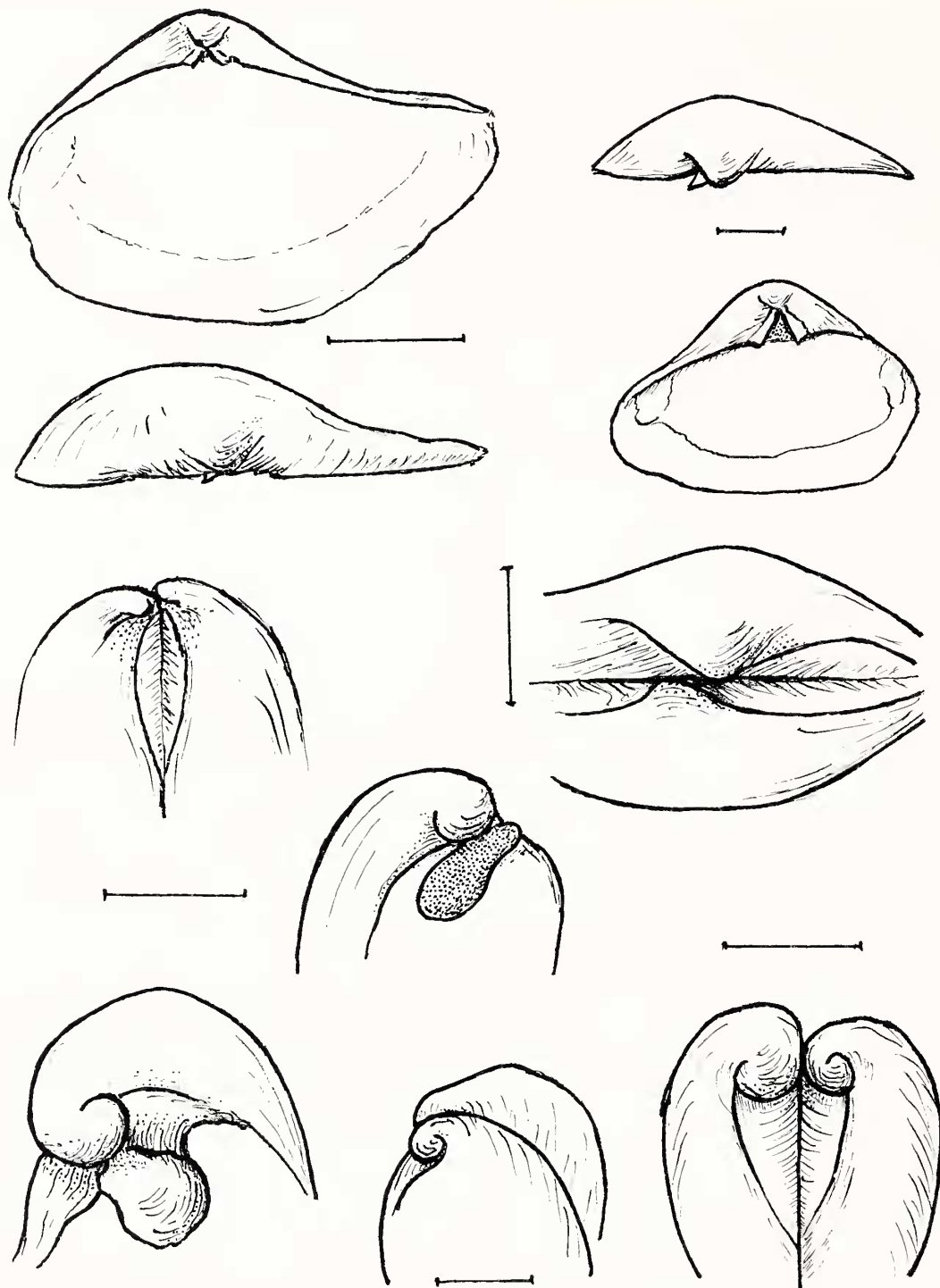


Fig. 8.—(upper left two) Internal and apical view of valve of *Erodona iquitensis*. (upper right three) Apical, internal views, and umbonal asymmetry in valves of *Erodona mactroides*. (lower five figures) Different views of umbo and hinge in *Anisothyris obliquus*. Scales represent 1 cm.

valves are very expanded posteriorly and the anterior end rounded; both adductor scars very shallow. The character that best distinguishes this species from *E. mactroides* is the contour of the posterior end of the valves which, in a profile view from the top (umbonal or dorsal view), is rather concave instead of convex. Lunule and escutcheon are well-defined and an obsolete, filiform ligament fits into the marginal line at both sides of the umbo.

I have seen numerous living and fossil specimens of *E. mactroides* showing great variability in shape, some posteriorly truncated and with strong dorsal carina, and others very rostrate as in *iquitensis*. Living *Erodona* have a brown dull periostracum, with some longitudinal blackish markings, sometimes in form of V's on the upper middle part of the valve; such characters, of course, cannot be detected on fossils.

Anisothyris iquitensis was described from a single valve from Iquitos, Peru, and only one specimen similar to it exists among the material from the Ecuadorian Miocene (CRB 7) of Basal Loyola. It might be that this peculiar shell represents a transition, or a subgeneric difference between *Erodona-Anisothyris*, and related to the true marine *Corbula* of the subgenus *Carycorbula*, but in any case it is closer to *Erodona*. True *Anisothyris* do not appear in Miocene materials, and the several species known of that genus are from the Pliocene of Peru.

Genus *Ostomya* Conrad, 1874

Himella H. Adams, 1860. Not *Himella* Dallas, 1854. Type *H. fluviatilis* Ad., 1860; Marañon River.

Ostomya Conrad, 1874. Type *O. papyria* Conrad; fossil of the "Pebas" Group.

Guianadesma Morrison, 1943. Type *G. sinuosum* Morrison; Cuyuni River at Kartabo, British Guiana.

Type species.—*Ostomya fluviatilis* (H. Adams).

Original description of *Himella*.—"Shell thin, inaequilateral, inaequivalve, left valve larger, closed, with a light constriction extending from the beaks to the ventral margin, covered with an epidermis; beaks tumid, obtuse. Hinge composed of an obscure tooth in the right valve, with a corresponding cavity in the left valve; ligament external, cartilage internal contained in a narrow, almost horizontal cartilage-process in each valve. Pallial line slightly sinuated." The (unfigured) specimen was from H. Cumings' collection obtained from Mr. Bates.

Original description of *Ostomya*.—"Thin, concentrically plicated; hinge with a spoon-shaped oblique fosset in the left valve and a small tooth near the apex. Right valve cartilage fosset very oblique, almost parallel with the hinge line." The author gave no dimensions of the type, but if the figured specimen (pl. 1, fig.

6) is of natural size, then it must correspond to a rather young specimen.

Original description of *Guianadesma*.—"Shell small, slightly inaequivalve, rhomboidal, translucent, nacreous porcellaneous within, furnished with a variously wrinkled epidermis. Hinge anodont. Ligament short, internal, opisthodontic, that is posterior to the beaks, on a narrow ledge; without an ossicle. Pallial line broad, shallow. Right valve emarginate postero-ventrally."

Comparison of the preceding descriptions shows that the three named genera belong to the same thing. Although Adams did not illustrate *H. fluviatilis*, it is, according to Pilsbry (1944), the same as *G. sinuosum* figured by him (pl. 11, figs. 42-44) for *O. fluviatilis*, and probably *O. papyria*, is also the same. This is also supported by Morrison's (1943) illustrations (pl. 8, figs. 1-6) with drawing of the general anatomy, and with the paratypes I observed in the collection of the Carnegie Museum of Natural History.

H. Adams (1860) referred his species to Corbulidae, "with greater affinity with *Azara*" and Pilsbry said it is one of the "several stocks of Corbulidae (*Erodona*, *Anisothyris*, *Ostomya*) that invaded freshwaters during the middle and later Tertiary in South America, but only *Ostomya* appear to have persisted as a purely fresh-water genus." We have seen that *Erodona* (= *Azara*) is also found in fresh-water stations in the Amazon. Although Morrison in his description of *Guianadesma* placed it with the Lyonsiidae, it is significant that his first impression in the preliminary report on the molluscs of Kartabo (a manuscript is in the file of the Section of Invertebrates at Carnegie Museum of Natural History) was that such a bivalve belongs to Corbulidae. The inclusion of *Ostomya* in that family, however, might present some questions, because it is byssiferous, living on rocks, has certain characteristics on the hinge line, and has a peculiar periostracum. One specimen from Tapajos River at Santarem, Pará, Brazil (CM, collected by Hase-man, 1909) has more overlapping valves, as in *Erodona*, and the seminternal ligament is at both sides of the umbo; these were found with *Congeria septa* Conrad.

Ostomya cf. *fluviatilis* (H. Adams)

Remarks.—One possible specimen is a left valve in Matrix CRB 26b of Basal Loyola that contains numerous *Neocorbicula*. The valve is more elongated than in the typical *O. fluviatilis* and the other fossils above mentioned. It probably is an earlier

chronological and allopatric form, but only can be fully described if new and better materials are found. Other fossil *Ostomya* are known from La Cira Formation of Pachitea River, Upper Oligocene-Lower Miocene of Peru—*P. terminales* Pilsbry and *O. pacchiteana* Pilsbry.

Class Gastropoda
Order Prosobranchia
Superfamily Trochacea
Family ?Trochidae

Matrix CRB 7 of Basal Loyola contains a cast that is a piece of a helicoid shell, which is the largest among other gastropod materials. It is only a basal fragment, apparently a trochoid. The cast is 10 mm wide, showing regular and fine spiral sulcations (5 in number), with the umbilicus very wide, deep, and smooth. This fragment of the base of a shell may correspond to *Calliostoma*, but no more can be indicated beyond this observation until more larger parts or complete specimens are found. (The cast in the matrix was filled with plastiline in order to obtain a better view of its shape.)

The matrix is probably the result of mixed marine and freshwater deposits, which contains *Hydrobia*—though this can be also brackishwater—in large quantities, and also the freshwater *Gyraulus*, casts of small Neritids, the problematic, bivalve-looking specimen mentioned on page 50, and unidentified Crustaceans.

Superfamily Neritacea
Family Neritidae
Subfamily Neritinae
Genus *Neritina* Lamarck, 1816

From the Neogene of Peru and Ecuador several species of *Neritina* have been described. The earliest one (Gabb, 1869) was indicated as from the Miocene (Boettger, 1878, assigned to the same deposits an Oligocene-Miocene age), but most authors placed these deposits in the Upper Tertiary-Miocene. Those from Pebas Formation in Peru are probably of Pliocene age, and some species survived in the Pleistocene of Brazil which was also indicated as "Pebas" until G. G. Simpson (1961) made the correction in 1961. *Neritina pacchiana* Palmer and the species described herein from Ecuador are the oldest species of the genus, and probably *N. pacchiana* is the precursor of *N. roxoi* from Pebas. T. R. Roberts (1975) also listed the genus *Theodoxus* from the same deposits, but this genus is only known from the Pliocene and Recent of Eu-

rope and Near East. *Neritina* aff. *amazonensis* de Greve was listed by Roberts from the Loyola Formation, but this Peruvian species, of considerable size, was not found in the materials studied here, which were collected by Bristow.

All the species can be differentiated, briefly, as follows (in older, Miocene, materials the external patterns indicated for those of Pebas, may not be observable):

Neritina roxoi de Greve.—Close to *N. ortonii* Conrad, with oblong color patches over a reticulated background.

Neritina pacchiana Palmer.—Similar to *roxoi* in coloration but thicker and with more pointed apex (upper part of the shell almost triangular).

Neritina ortonii Conrad.—(New name for *N. pupa* Gabb not Linnaeus.) Smaller with well separated ziczac axial lines.

Neritina etheridgei Roxo.—(New name for *N. ziczac* Etheridge not Linnaeus.) Larger, globose, with columellar area concave and numerous waved lines.

Neritina amazonensis de Greve.—Similar to *Etheridgei* Roxo, but with flat apex and without color lines.

Neritina puncta Etheridge.—Similar to *amazonensis*, but with spiral lines of dots instead of waved ziczac lines.

All the above listed species (except *N. pacchiana*) are from the Pliocene of Peru, of globular shape, and different from the *Neritina* of the Miocene of Ecuador.

Neritina loyolaensis, new species
Fig. 9, 10, 11

Holotype.—CM 46790, collected by C. R. Bristow (CRB 9) at Descanso, Entrance of Tahuallcanyon, in Basal Loyola Formation; 6 paratypes, in British Museum GG 19827, and 19862.

Description.—Shell higher (25%) than wide, with a spire that corresponds to about one-third of the body whorl. Well defined suture. Shape similar to the Recent *N. virginea* (L.) but with more acute apex as in *N. reclinata* Say. Body whorl marked, in dorsal view, by alternate dark and clear bands of equal width; on the upper part of the whorl these bands are narrower, becoming slightly wider toward the base; the bands begin obliquely toward the right, and by the middle of the whorl form an acute angle, turning to the left in ziczac pattern; near the base they become almost vertical and parallel. The bands are also strongly marked as to give the appearance of a sulcated surface. The base is oblong, not globose as in other fossil species. Length of the shell 9.4 mm; diameter 7.3 mm; last whorl 6.3 mm from suture to base.

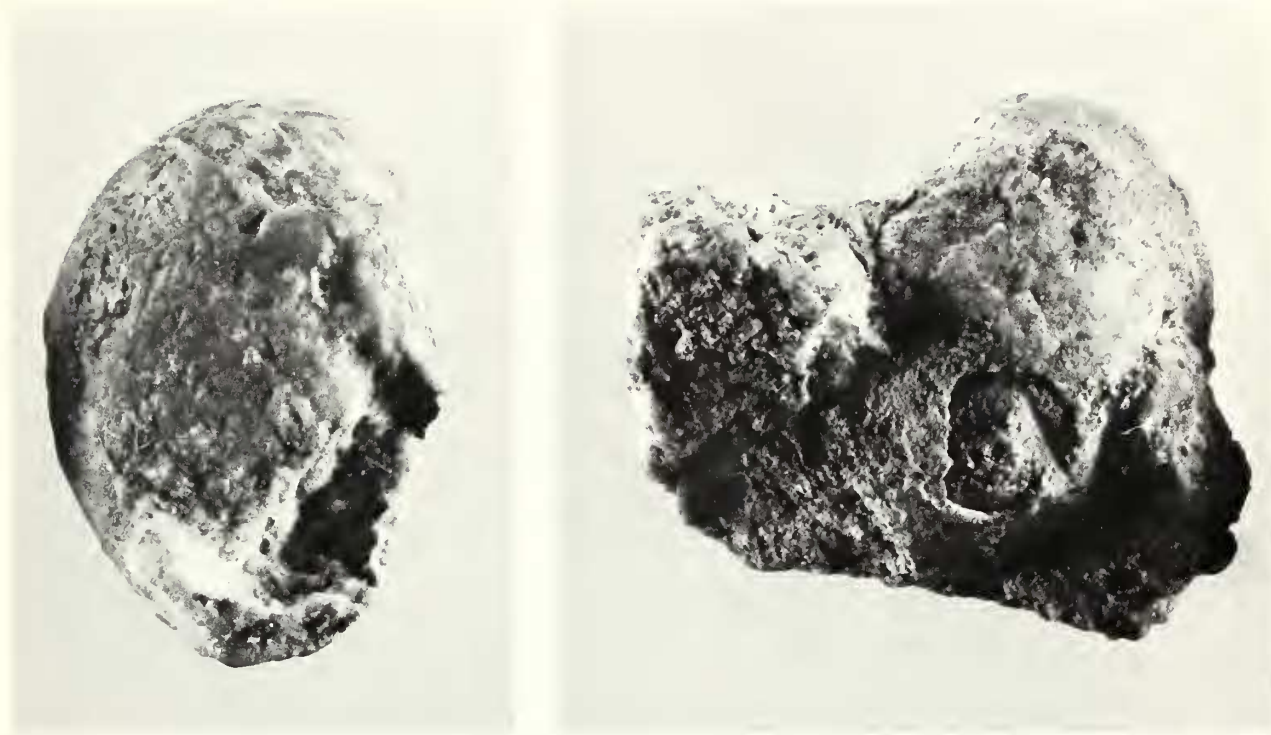


Fig. 9 (left).—*Neritina loyolaensis*, new species holotype (CM 46790). Basal Loyola Formation, at Descanso. $\times 7\frac{1}{2}$.
Fig. 10 (right).—Same, paratype in matrix (CM 46790a).

Variations in markings.—In other specimens besides the above described holotype, one is larger (12.5 mm high) with the bands near the suture running almost parallel. Another in the same matrix is a fragment of the shell showing more of the portion toward the lip, where the bands are broken into irregular oblong spots in a manner similar to that in *N. pacchiana*.

Comparisons.—*N. loyolaensis* differs from *N. pacchiana* by being considerably more elongated (*pacchiana* is as wide as high) and in the color pattern (*N. pacchiana* shows only triangular patches without any axial banding). *N. pacchiana* has a lower apex. From *N. ortonii*, *N. loyolaensis* differs by its more numerous bands, not waving but of regular ziczac pattern, and being not globular, larger, and with much higher apex.

N. loyolaensis can be easily separated from the other *Neritina* listed above from the Neogene. Color pattern in species of this genus is variable; if it would be possible to assume that it represents a peculiar variation of *N. pacchiana*, the criterion, then, to differentiate the other species would be invalid; all the species are distinguished by their peculiar shape, and altitude of the spire as well as the pattern (coloration pattern in *Neritina* is a feature fairly well preserved in Tertiary fossils). *N. loyolaensis*

is stratigraphically older than *pacchiana*, and even more so than the other Neogene species from eastern Peru.

N. loyolaensis belongs to the subgenus *Vitta* Mörch 1852, of which *Neritina (Vitta) virginea* (L.) is the type species.

Neritina pacchiana Palmer 1941

N. pacchiana Palmer, 1941, Bull. Amer. Paleontol., 100:396, pl. 9, figs. 3–4.

Type locality.—(This locality is not indicated with the description but it is inferred from the preliminary remarks by Palmer in previous pages) “Near Paccha,” Quebrada Paccha (float in stream beds) Areniscas (sandstones) of Azogues. This is above Loyola Formation (Guapán?) in the Miocene-Pliocene of Ecuador. Holotype in Paleontology Research Institute, Ithaca, New York, no. 4009.

Original description.—“Shell small, spire slightly elevated, columella callus thickened, more so anteriorly. Surface with bands of dark patches, irregular in size, some part of the shell compactly covered with dark spots. The coloration is described from one specimen, the only shell retaining such features. The



Fig. 11.—*Neritina loyolaensis*, new species (paratype BM GG 19827/1). $\times 3$.

coloration is closest to that of certain color variations of *N. virginea* L. of the West Indies and Brazil. Since the species of *Neritina* offer a wide variation in surface color markings, the pattern of one shell would not be enough for specific identification. The shape of the species differs from the 5 fossil forms of the Upper Amazonian fauna in being more erect, *i.e.* the spire is above the line of the posterior margin of the aperture and not at the same level with it. *N. pacchiana* does not have the spire elevated so much as the Recent *N. virginea* L. Height 6 mm; greatest diameter 4.5 mm."

Remarks.—Although this species is identifiable by its description and illustration, specimens from other localities cannot be assigned correctly to it; most of them belong to *loyolaensis*, which has a different shape as well as color markings.

Neritina sp.

Fig. 12

Remarks.—Internal casts of globular small individuals, 4 by 4 mm, were found in the matrix of coarse conglomerate of the samples of CRB 7, Basal Loyola Formation, which also contains Hydrobiidae and *Neocorbicula*. It apparently belongs to the *N. ortonii* Conrad complex, approaching that species in size, but cannot be identified as that species, which is from the Pliocene.

Other, unidentified casts from Upper Loyola at Malpaso (CRB 30), which Roberts (1975) indicated as *Theodoxus* (an Asiatic genus), are more likely *Neritina*.

Genus *Puperita* Gray, 1857

Type species.—*Nerita pupa* Linnaeus.



Fig. 12.—*Neritina* sp. Matrix that contained the specimen isolated below (of the *N. ortonii* complex). Basal Loyola Formation. Carnegie Museum specimen. $\times 6$.

?*Puperita* aff. *sphaerica* (Olsson and Harbison, 1953)

Fig. 13

[*Neritina*] *sphaerica* Olsson and Harbison, 1953, Monogr. Acad. Nat. Sci. Philadelphia, 8:340, pl. 60, fig. 6a–c.

Remarks.—Living *Puperita* can be distinguished from *Neritina* by their more roundish, "naticoid" shell, lack of denticulation on the inner lip, and the surface patterns. In Tertiary fossils, especially those of small size, the only dependable characteristic is the shape. The "*Neritina*" *sphaerica* described from the late Pliocene of Saint Petersburg, Florida, still shows a pattern of coloration with oblong spots, recalling that of the Miocene *N. pacchiana*; its authors suggested that most probably it belongs to the subgenus *Puperita* (by others considered as a separate genus); also they said that the species has weak columellar denticulations, a



Fig. 13.—Matrix from (CRB 48) Basal Loyola, with steinkern of *Puperita* aff. *sphaerica*. On the lower part the matrix also shows a portion of a valve of *Neocorbicula cojitamboensis* (CM). $\times 11$.

character of *Neritina*. The transition of color pattern—and somewhat also in the shape—from *Neritina pacchiana* to *sphaerica* and the living species, seems to indicate that, in the Neogene the generic separation was still in the process.

Our specimens, from localities 46 and 48, of Basal Loyola, are steinkerns, some still in the matrix. As usual in cases of inner casts, the sutural groove appears deeper than in those better preserved speci-

mens of *N. sphaerica*; the difference is noticeable enough to presume a specific distinction, even if they are of the same shape and size; a formal description under such a conclusion can only be made when better material may be obtained. On this occasion they are just indicated as “affinis” *sphaerica*. One of the specimens (CRB 48 in matrix) is about 5 by 4 mm, a little larger than the type of *sphaerica*; all have three whorls, the last enlarging

rapidly. The matrix contains also *Neocorbicula co-jitamboensis*.

Superfamily Cyclophoracea

Family Aperostomatidae

Genus *Poteria* Gray, 1850

Platystoma Mörch, 1850, not Meigen, 1803.

Subgenus *Pseudoaperastoma* Baker, 1943

Neocyclotus—in part—Crosse and Fischer, 1886.

Type species.—*Cyclotoma inca* d'Orbigny. (See remarks in Parodiz, 1969:103.)

Poteria (Pseudoaperastoma) bibliana

(Marshall and Bowles)

Fig. 14

Pomacea bibliana Marshall and Bowles, 1932:4, figs. 4–5.

Poteria (Pseudoaperastoma) bibliana, Parodiz, 1969:103, pl. 16, figs. 2–3.

Type locality.—Biblián sandstone of Cañar (= Basal Loyola Formation) found together with *Dor-yssa bibliana* and *Diplodon (E.) guaranianus biblianus*.

Remarks.—The shell of this species is very similar to the Recent *Poteria inca*; it has three to four whorls rapidly increasing in size. Spire flat and the body whorl composes most of the shell. Periphery almost carinated. Aperture widely expanded. Above the angulosity of the last whorl it is decidedly convex, and it descends obliquely below towards the base of the aperture. It is two thirds wider than high. Height 20 mm, width 30 mm.

Because *Poteria bibliana* is an operculated, terrestrial gastropod, the specimens must have been drifted into deposits that contain truly freshwater species. Our observed specimens are from locality CRB 26, of Basal Loyola.

Superfamily Viviparacea

The two families, Viviparidae and Ampullariidae, in this superfamily are both found with fossil representatives in South America, but are of different origins. While the Viviparidae (*Viviparus-Lioplacodes*) were found with certain abundance in the early Paleocene of Patagonia and Brazil they became extinct afterwards, there or elsewhere on the continent. Ampullariidae, with fossils in the middle and late Tertiary of the northwest, reached the southern regions in more recent times, not older than Pleistocene, and none living in Patagonia; they probably belong to an ancient stock probably related to the African genera, in the same manner as the

Mutelacea. The extinct South American Viviparidae, on the other hand, were more closely related to those of North America, or from the Old World.

Family Ampullariidae

Genus *Pomacea* Perry and March, 1810

Ampullaria Lamarck, 1810, not Lamarck, 1799 = *Pila* Bolten, 1798.

Ampullarius Montfort, 1810 (after March).

Pomus H. and H. Adams, 1856.

Ampullarius Parodiz, 1969:109.

Type species (of both *Ampullarius* and *Pomacea*).—"Nerita" *urceus* Müller.

Subgenus *Limnopomus* Dall, 1904

Type species.—*Ampullaria columellaris* Gould.

Pomacea (Limnopomus) manco Pilsbry

Fig. 15

Pomacea manco Pilsbry, 1944:145, pl. 11, figs. 31–32. Boss and Parodiz, 1977:116.

Ampullarius (Limnopomus) manco, Parodiz, 1969:110.

Type locality.—Quebrada de Sungarillo, in strata with "*Hemisinus*" *paleus*, Oligocene of the Pachitea River, Peru. Type in Academy of Natural Sciences, Philadelphia.

Original description.—"The shell's internal cast is globular, umbilicate, with a moderately elevated spire. The last whorl is very convex. The aperture is semilunar, rather narrow. L. 15.5 mm (Type), D. 14.5 mm. Another specimen D. 16 mm."

Remarks.—One specimen, CRB 34, of Basal Loyola, has great affinities to, and it is, tentatively, assignable to this species. The type of *P. manco*, being umbilicate, shows a probable transition with the subgenus *Effusa*. This species is small in size in comparison with some of the other fossils (*P. prourceus* Boss and Parodiz) and the living species (*P. maculata* Perry = *gigas* Spix), which are giants among the freshwater operculated snails.

The Oligocene age of *P. manco* is still questionable; very similar species as *P. guadasensis* (Anderson) from the Magdalena Valley in Colombia are not older than Pliocene, and probably Pleistocene, instead of early Tertiary as indicated by Anderson.

Superfamily Rissoacea

Family Hydrobiidae

The family name Hydrobiidae, as used by most authors in a broad sense, contains an array of subfamilies that may, or may not, correctly belong to it, but may constitute distinct families—Hydro-

biinae s.s., Lyogyriinae, Littoridininae, Amnicolinae, Benedictinae, Lithoglyphinae. Although the Hydrobiidae are related to the marine family Rissoidae, they differ in certain features, as in the operculae, the presence or absence of accessory tentacles, the radula, and embryologically, because the Hydrobiidae do not have the free-living larvae of the marine forms.

In spite of Opinion 457 (1957) of the International Commission of Zoological Nomenclature, in support of Bitynidae Gray, 1857, as the valid name for the family, the consensus of most authors disregards such rule, using Bulimidae (= Bithynbiidae) as a separated family from the real "Hydrobias." Recent anatomical studies help to clarify the relationship of the groups within or segregated from the family. However, in fossils in which only the shell or casts are known, the taxonomic difficulties persist. The assignment to particular subfamilies or genera, inferred by shell comparison with the living taxa, cannot be certain in all cases.

Hydrobia is a genus considered to be restricted to the Northern Hemisphere and to be replaced in South America by groups more commonly placed in the Littoridininae. However, there are some species in South America, especially those of brackishwater environments that appear to be more closely related to *Hydrobia* than to *Littoridina* or others of its group.

Genus *Hydrobia* Hartmann, 1821 (sensu lato)

Hartmann in Sturm's Fauna Deutschland, Abd. 6(5):46.

Type.—*Helix acuta* Draparnaud, subsequent designation by Gray, 1847.

By the shell alone, the differentiation in certain species between *Hydrobia* and *Littoridina* is difficult, and this is even more of a problem in fossils. These two genera are very similar in shape, and both are devoid of sculpture in the adults. I have compared several of the living species, abundant in La Plata River system, identified as *Littoridina*, and found that the named *L. australis* differs from the others of the estuary, not living in freshwater but always in brackishwater, and can be assigned better to *Hydrobia* (this genus taken in a broad sense). The similarity of shape, smooth surface, and flattened sides of the whorls, of the species *australis* with *Hydrobia ortonii* of the Neogene of Peru and Ecuador, indicates that both must belong to the same genus.

?*Hydrobia ortonii* (Gabb, 1869)

Mesalia ortonii Gabb, 1869, Amer. J. Conchology, 4:198, pl. 16, fig. 3. (*Mesalia* Gray, 1842 is a Turritellidae.)

Isaea ortonii Gabb, 1871.

Hydrobia (Conradia) ortonii, in Wenz, 1938. De Greve, 1938:90.

Hydrobia (Isaea) confusa Boettger, 1878. De Greve, 1938:90.

Hydrobia (Conradia) confusa, in Wenz, 1938. De Greve, 1938.

Type locality.—The type locality was indicated in the introduction of the paper by Gabb (1869): "high bluff at Pebas, on the Ambiyacu River, two miles above its confluence with the Marañon, near the southern border of Ecuador."

Original description.—"Shell small, elongated, spire high, whorls eight or nine, sometimes very plain, or in other cases marked by two or more revolving carinae in the young state, which always disappear as the shell grows older; the larger whorls are smooth, flattened on the sides and round in above and below, to the suture, which is deeply impressed; base of body whorl rounded. Aperture subovate, acute behind, rounded in advance; outer lip thin and straight, inner lip acute and slightly reflected over the umbilical region. Dimensions.—Length .35 in., width .13 in."

Remarks.—De Greve placed all the Pebas species in *Hydrobia (Conradia)* but these correspond better to *Dyris*, except *ortonii* which does not belong to this group of sculptured shells. Its assignment to *Hydrobia* is acceptable, *sensu lato*, provided it is understood that the *Conradia-Dyris* group is excluded.

Numerous specimens and fragments of this species are contained in the gray shales of loc. CRB 7 (Loyola Formation); some of these appear to have more impressed sutures and the whorls more convex because they are internal casts. However, these differences are the same as seen in the original figures in Gabb (1869) in comparison with those photographed by de Greve (1938), and indicate also that there is no clear distinction between *ortonii* and *confusa*. The specimens from the Loyola Formation might correspond to a different form, due to their age and location, but apart from some of them being slightly more elongated, there are no other features or characteristics that can be described. For other ?*Hydrobia* sp. from the locality CRB 7 (Basal Loyola) reported by Roberts (1975:262) see *Lyrodes*.

In matrix of the locality CRB 7, of Basal Loyola, a few casts of *Hydrobia ortonii* were observed. This is the same matrix that contains the marine fragment of the already mentioned ?*Calliostoma*, and also the fish scale with a bivalve-like appearance. This is another indication of the more salobre condition in which *Hydrobia ortonii* lived.

Genus *Liris* Conrad, 1871

Type species.—*Liris laqueata* Conrad, 1871, Amer. J. Conchology, 6:194.

Original description.—"Elongated, subcylindrical, with convex whorls and oblique longitudinal ribs; apex entire; aperture suboval, small, peristome continuous, labium reflexed and prominent. This may be only a subgenus of the former [*Isaea* = *Dyris*], but the shell has a more general resemblance to *Pupa* and is without an umbilicus. The aperture proportionally smaller."

Wenz (1938) placed *Liris* within the subfamily Littoridininae, although the taxonomic position of certain genera of Hydrobiidae is still provisional. *Liris* contains species which, as the type species, have only longitudinal ribs, but others, as *L. tuberculata*, have a more decussated sculpture, and are scalariform. This genus has also certain resemblances with *Prososthenia* Neumayr from the Pliocene of Europe, but *Prososthenia* is very irregular in shape, has more oblique sutures, and has a strong peristome. The two genera are typical, however, as an example of great variability in many similar groups of Hydrobiidae.

Liris minuscula (Gabb, 1869)

Turbonilla minuscula Gabb, 1869, Amer. J. Conchology, 4:197, pl. 16, fig. 1.

Liris minuscula, de Greve, 1938:92, pl. 1, figs. 31-35, pl. 2, figs. 1, 9, 11, and text figs. 12-18. Parodiz, 1969:120.

Potamides "n.sp.," Bristow and Hoffstetter, 1977:337.

Type locality.—The type is from the Pliocene of Iquitos, Peru.

Original description.—"Shell minute, elevated, slender; whorls six or more, rounded, suture deep; surface marked by about fifteen rounded, longitudinal ribs, with concave interspaces; aperture subcircular, outer lip simple, straight, inner lip slightly thickened."

The figured type (in the Academy of Natural Sciences, Philadelphia) is a specimen with only the last 4 whorls, broken at the apex; it measures 3.7 mm in length and 1.9 mm. wide.

Remarks.—The axial sculpture of this species shows great variation in the development of the ribs, which in some specimens are very strong, and with the greater convexity of the whorls and deep sutures, the shells take a scalariform aspect. Such variations were profusely illustrated by de Greve (1938). This species is characterized also by being entirely devoid of spiral sculpture. It is close to the type of *L. laqueata*, but that species has a still deeper suture, with the peristome completely detached from the body whorl similar to that of the Clausiliidae, and it is produced. The specimen of

laqueata, in fig. 21 of de Greve (1938), looks like an intermediate with *minuscula*.

The examined specimens are from the lots PH1 and PH2, localized at Lat. 0°29'N, Long. 78°3'W, and Lat. 0°28'N, respectively, from the Tumbatú Formation (Neogene) and also from San Cayetano Formation. They are contained in a matrix of solid "coquina" and are represented by numerous fragments of crushed shells and also some complete specimens. The coquina looks as if it had been formed by brackishwater, rather than freshwater sedimentation. Because the species was originally described from the brackishwater fauna of Iquitos, Peru, probably the older Ecuadorean populations lived in similar environments, or might have been accumulated on the strand by drift. Parts of the coquina are covered with hardened clay that may be younger than the matrix, although it also contains the species. One specimen in it is of considerably larger size (about 8 mm long) and it is entirely calcified.

Genus *Dyris* Conrad, 1871

Isaea Conrad, 1871, not Edwards, 1830.

Conradia Wenz, 1925, not A. Adams, 1860.

Type species.—*Dyris gracilis* Conrad, 1871:195.

Original description.—"Subulate, with many volutions; aperture ovate, labium reflexed. The mouth of this shell is similar to that in the genus *Melania*, but the form and sculpture of the shell are very different from those of *Melania*."

Conrad's description of this genus is very insufficient, and it can only be identified by complementing it with the description of the type species from the Pebas Formation in Peru. The principal characteristic of the genus is the lack of axial sculpture, but it is also characterized by strong spiral ribs carinae-like, the elongated spire, very deep suture, and relatively small aperture. Among living genera it resembles *Calipyrgula* and *Lyrodes* in shape. Several species have been described from Pebas, and recognized by de Greve under *Hydrobia* (*Conradia*). The variability of such species is so great and their intergradations so many, that for the purposes of correct identification only two species can be considered—*ortoni* (Gabb) = *confusa* Gabb, and *Dyris gracilis* Conrad, which includes *tricarinata* Boettger and *D. lintea* Conrad. It has already been seen that the larger species—*ortoni*—with less marked suture and without sculpture does not belong to the same *Hydrobia* (*Conradia*) group in the sense of de Greve (equivalent of *Dyris*), but to a more *Littoridina*-like *Hydrobia* (sensu lato).

Dyris gracilis Conrad, 1871

Dyris gracilis Conrad, 1871, Amer. J. Conchology, 4:195, pl. 10, fig. 8.

Type locality.—(referred to in the introduction of the paper) 30 miles below Pebas, on the south side of the Marañon, at Pichua, just west of Cochaquinas; "the shells appear to be even more abundant than at Pebas." 30 miles below Pebas is in the direction of Iquitos, from where the abundant material studied by de Greve came, but still far from it.

Original description.—"Very slender and elongated; whorls 8, convex, revolving lines carinated, very regular, 4 on the penultimate and 5 on the last whorl; about the sutures there is rather wide indented space, whorls minute and obliquely striated. The figure is a rough outline, merely indicating the natural size." [The "indicated" size is 8 by 1 mm.]

Remarks.—In typical *D. gracilis*, the flat space between the sutures is sometimes as wide as the rest of the whorl that is ribbed, but in others that space narrows. Those with wide spaces correspond to the form *tricarinata* Boettger, with the three ribs in the remainder of the whorl very conspicuous. Between this condition and the normal *gracilis* there are many intergradations and the two forms cannot be separated clearly; gradual variations continue until the interspace completely disappears, becoming the form that was named *lintea* by Conrad; this modification is accompanied by a widening of the base.

In comparison with the abundance of specimens found at Pebas, those of the Upper Miocene of Ecuador (San Cayetano Formation—Loja) are scattered impressions on the surface of the shales, collected by Bristow and Kennerley (JW 424) and are mostly of the *tricarinata* form. This is perhaps the ancestral form of *gracilis* from which the Pliocene polytypic populations evolved.

Professor C. Carrion collected for the British Museum, at the same locality of Loja, two small slabs of very pale buff silty limestone with impressions of the same species mixed with remains of *Characea* (British Museum G 43325–6).

Genus *Lyrodes* Doering, 1885

Potamopyrgus (in part of authors for Neotropical species).
Pyrghophorus Ancey, 1888.

Type species.—*Lyrodes guaranítica* Doering, 1885, Bol. Acad. Nac. Cien. Córdoba, 7:461–462.

Type locality.—"Lagunas riberenyas" (small lakes on side of the river) near Barrancas River

(tributary of Guayquiraró River, on the border of the Corrientes-Entre Rios provinces, Argentina). The type, from Doering's collection at the Academy in Córdoba, was lost; a neotype was selected by Parodiz (1960:25) from Riachuelo, near Corrientes city (CM 59-108).

Lyrodes sp.

Remarks.—From locality CRB 7 (Basal Loyola), internal casts that are different from the other Hydrobiidae may be assignable to *Lyrodes* (the same were indicated as *Hydrobia*? by Bristow, 1973:23). They measure about 3.5 mm in length and have rounded whorls with deep sutures. Separated from the matrix, one incomplete specimen has three whorls which when entire, must have been more than 4 mm; it shows very convex whorls of rapid growth which is characteristic of the genus. For their size and shape, the specimens can be compared with *Lyrodes lacrianus* (Pilsbry and Olsson, 1935:9, pl. 5, fig. 6), but this is a much older species from the Upper Oligocene of Colombia in La Cira Formation (see also Parodiz, 1969:117). Although belonging to the same group, the Ecuadorean sample must correspond to a different species, which may be described when more and complete specimens can be obtained. The matrix is the same one that contains the "problematic fossil" (probably a fish scale) that looks like a minute pectinid valve.

Genus *Toxosoma* Conrad

Pseudolacuna Boettger, 1878:496.

Type species.—*Toxosoma eborea* Conrad, 1874:31, pl. 1, fig. 7.

Original description.—"Conical, polished, the aperture projecting, subovate, direct, peristome continuous; columella concave with a plait or tooth in the middle, not oblique, base rounded, subumbilicated."

Toxosoma eboreum Conrad (emend. Pilsbry, 1944)
Fig. 16

T. eborea Conrad, 1874; Tryon, 1883:270; Pilsbry, 1944:151, text fig. 3a–b (name changed to *eboreum* because of the ending of the genus name, *soma*, in this regard see ICZN Article 30a; Parodiz, 1969:121).

Pseudolacuna macroptera Boettger, 1878:496, pl. 13, figs. 1a–15 (Pebas); Oliveira Roxo, 1943:638, pl. 29, fig. 25; de Greve, 1938:74, pl. 5, figs. 17–18, 24–29, 31–36.

Hydrobia (Paludestrina) dubia Etheridge, 1879:86, pl. 7, fig. 11 (the author said that he named it with much doubt); Oliveira Roxo, 1943:640–641, pl. 29, fig. 24 (as *Isaea*).

Type locality.—Pebas (Pliocene), Peru.

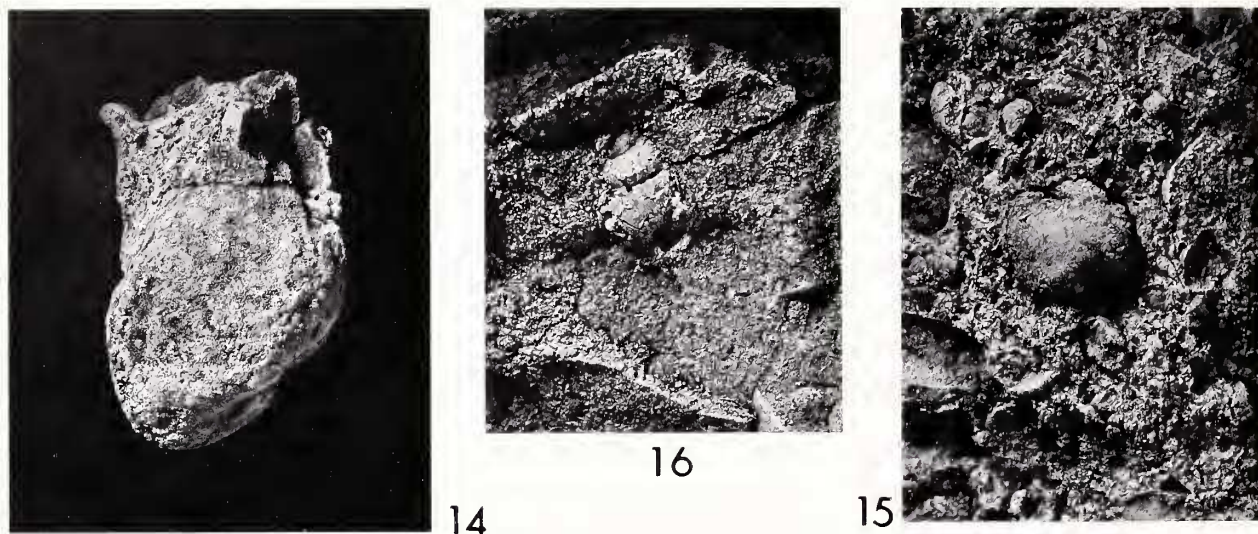


Fig. 14.—*Poteria* (*Pseudooperastoma*) *bibiana* (BM GG 19821). Basal Loyola Formation. $\times 2$.

Fig. 15.—*Pomacea* (*Linnopomus*) *manco* (BM GG 19819). Basal Loyola. $\times 4$.

Fig. 16.—*Toxosoma eboreum* (BM GG 19816). Mangán Formation. $\times 5$.

Remarks.—Conrad's diagnosis is very brief, indicating that it is small (4.7 mm) with 5 whorls rounded, aperture angular above, last whorl expanded, and with a minute columellar tooth. The figure, although very small, is recognizable as being the same as *P. macroptera*, which Pilsbry verified when he redescribed the type in the ANSP (161152). The dimensions are approximately the same, and de Greve specimens are even smaller.

The fact that this species was frequently referred to as *macroptera* does not make *T. eborea* a "nomen oblitum," as the rule for that was not applied before 1960 and, more important, it was not overlooked; de Greve listed it (1938:5) among the Conrad species of 1874, but failed to recognize its identity. De Greve listed also *Hydrobia dubia* Etheridge (1938:8, 10) but did not include it in the synonymy or the systematic discussion of the species. The figs. 24, 29, 33–34 on pl. 5 show specimens of the variations of *macroptera* which are identical with the form described by Etheridge.

T. eboreum is extremely variable in the development of the last whorl and peristome; the columellar tooth sometimes is absent or so internally placed (in fact it is a fold that continues on the internal columella) that it can be seen only in an oblique view of the shell.

Our specimen (British Museum GG 19816) is from locality CRB 26b, in matrix from Mangán Formation. It gives a front (apertural) view of the shell

which has a large body whorl; the penultimate whorl has an adherence that gives the false impression of being carinated but the surface is smooth. The last whorl occupies two-thirds of the length of the shell (length 4.5 mm, width 2.5 mm). Length of the aperture is approximately half of the shell diameter. Width of the aperture is 1 mm. The specimen agrees with those illustrated by de Greve (1938) in figs. 29 and 34. As for the spire, all the specimens figured as *P. macroptera* are the same.

This species has similarities with "*Lacuna*" (*Ebora*) *crassilabris* Conrad (which is probably a *Toxosoma*) but it is much narrower, with a shorter spire and angulated, instead of rounded, aperture.

Genus *Potamolithoides* Marshall and Bowles, 1932

Type.—*Potamolithoides bibianus* Marshall and Bowles, 1932:4, figs. 1–3.

Original description.—"Shell small, resembling *Potamolithus* but with spire depressed and base widely umbilicated or deeply excavated."

Potamolithoides bibianus Marshall and Bowles, 1932
Fig. 17

Potamolithoides bibianus Marshall and Bowles, 1932:4, figs. 1–3. Parodiz, 1969:116, pl. 17, figs. 1–2.

Holotype.—National Museum of Natural History, 312840.

Remarks.—The characters of the genus are better

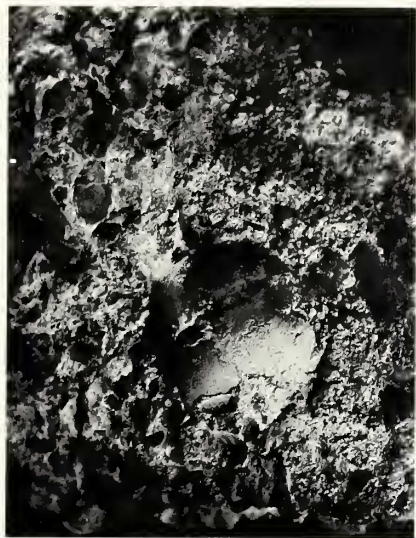


Fig. 17.—*Potamolithoides biblianus* (BM GG 19818). Basal Loyola. $\times 3$.

indicated in the description of the type and only species. It is of small size (3.5–5 mm by 5–7 mm), apical whorls slightly sunken, whorls flatish above and subangular at periphery, base flat, and aperture oblique with thin lip.

The figures of the type do not show the flatness on the upper part of the whorls, as the description indicates, but the outline is rather regularly convex, without angulosity. The whorls increase with regularity, and the last one is expanded on the outer part near the peristome, a character for which the authors found resemblance with *Potamolithus*. In most *Potamolithus*, however, the apex is rather prominent; in very few forms, as in *Potamolithus lapidum paysanduanus* (Pilsbry), the apex is very low, but not sunken. By the characteristics of the last whorl, *Potamolithoides* is also comparable to *Eubora* Kadolsky, 1980 (new name for *Ebora* Conrad) but in this genus the apex is conspicuously elevated as in *Potamolithus*.²

Our specimen, from CRB 26b of Basal Loyola (British Museum GG 19818), is embedded in the matrix, showing only the last whorl, very similar to the fig. 3 of the type of *Potamolithoides biblianus*. It is assignable to that species (Fig. 17).

² When this manuscript was completed, an article by Dietrich Kadolsky appeared in *The Veliger*, 22:364, April 1980, in which the taxonomic position of *Eubora* and *Toxosoma* is discussed. It corroborates our previous indication of *Pseudolacuna macroptera* as synonym of *Toxosoma eboreum* and gives a revision of this species from the Pliocene of Peru, with complete references. It also shows the great similarities of *Eubora* (ex-*Ebora*) with some of the many species of *Potamolithus* now living in the Uruguay River.

Superfamily Cerithiacea

The living freshwater Cerithiacea, which formerly were included in the whole embracing "family" group of the Melanians, offer some taxonomic difficulties for the separation of families, subfamilies, and even genera. According to Morrison (1954) they were derived from three different marine family stocks. The two distinguishable groups in South America belong to Thiariidae in which many species are considered as being parthenogenetic, and Pleuroceridae, which are dioceous, and both differ also in the mechanisms of oviposition. Because such conditions are not possible to verify in fossils, the placement of the genera within the families is inferred only by characteristics and relative similarity of the shells.

Family Pleuroceridae

Subfamily Potadominae (=Melanatriinae)

Genus *Doryssa* H. and H. Adams, 1854

Sheppardiconcha Marshall and Bowles, 1932.

Type species.—*Melania atra* (Brüguiere, 1792).

Original description.—"Shell subulate, turreted, spire decolled, whorls longitudinally plicate and decussated with transverse ridges; aperture subcanaliculated in front; outer lip incrimated."

Remarks.—This taxon was originally described as a subgenus of *Vibex* [!] Oken, 1815, but its author must have had in mind *Vibex* Gray, 1847, a synonym of *Pachymelania* of West Africa, a Thiariidae.

When the genus *Sheppardiconcha* was described with the species *S. bibliana* Marshall and Bowles as type, the authors considered it to be of an age no later than Pliocene or even earlier. They gave only a brief diagnosis for *Sheppardiconcha*: "turretiform spire, roundish aperture which is apparently somewhat produced at the columellar side." It was also suggested by the authors that "*Hemisinus*" *tuberculifera* Conrad was an allied species of *Sheppardiconcha*, but Conrad's species is a Thiariidae of the genus *Aylacostoma* (*Hemisinus*), which is devoid of axial sculpture, which in *Sheppardiconcha-Doryssa* appears as conspicuous sigmoid riblets. The characters of both *Doryssa* and *Sheppardiconcha* are identical, and because of that Morrison (1954) placed *Sheppardiconcha* as a synonym of *Doryssa*.

Older *Doryssa*, *D. maymarensis* (Bonarelli), were abundant in the early Tertiary of South Amer-

Doryssa bibliana (Marshall and Bowles)

Fig. 18

Sheppardiconcha bibliana Marshall and Bowles, 1932:3, pl. 1, fig. 6.

Henúsinus (*S.*) *biblianus*, Palmer, 1941:40, pl. 6, figs. 1-2.

Doryssa bibliana, Parodiz, 1969:134, pl. 15, fig. 12.

Type locality.—Biblián, Prov. Cañar, Ecuador, Lower Miocene. The type is in the National Museum of Natural History.

Original description.—"Shell turritelliform imperforate, whorls numerous [the type specimen with broken apex has 6½ whorls; the entire shell must have had 10-11 whorls], slowly increasing in size, somewhat flattened, longitudinal sculpture consisting of sinuous, slightly protractive incremental striae. Spiral sculpture of five strong, obscure nodulous lirae on the surface of the whorls of the spire and one sunk in the suture. Base worn but showing the remains of several lirae. Aperture roundish, columella curving forward." Length (upper whorls missing) 20 mm. Diameter 8.5 mm.

Remarks.—Palmer found this species to be abundant in several localities between Azogues and Pacha. Our observed specimens, especially those from Loyola Formation, show a series of variations from the type. In some the whorls are more convex, the suture conspicuously canaliculated and followed by a narrow shoulder, and the sigmoid lines or riblets may be stronger so as to form a characteristic axial-oblique and thick sculpture broken at the top into tubercles. Other specimens show variations (see list below) among the series and also from the type. Those figured previously (Parodiz, 1969: pl. 16) show also the variations in figs. 6 and 8, but that of fig. 12 (which corresponds to one figured by Palmer) is an extreme one, with the axial riblets obsolete, and it is probably a "temporal cline."

The spiral sculpture begins about the middle of the whorls, merging with the axial ridges and, on the lower part becomes more regular, so that the last three, above the suture, are stronger and parallel. The columellar lip at the aperture has in some specimens a distinct callus and is concave at the base. It seems that the sigmoid incremental ridges became proportionally stronger from the populations of those of the Lower to the Upper Miocene. It would not be of any taxonomic value to designate by name the younger populations as if they were chronological forms (what Simpson calls "successional" subspecies) because such variations are recurrent in all the Miocene strata and the extremes are linked by numerous intermediate individuals.

A related species, derived probably from the



Fig. 18.—*Doryssa bibliana* (CM 46791). Mangán Formation. $\times 6$.

ica in the Puca Formation. This species is also known from the Tejon Formation, Eocene of California. The living species of *Doryssa* replace *Pachychilus* (most common Central American Pleuroceridae) as you move southwards in South America.

same stock of the Pliocene at Iquitos, Peru, "*Cerithium*" *coronatum* Etheridge (which is *Doryssa*), is also highly variable, as was illustrated by de Greve (1938), but, in general, the axial incremental sculpture is reduced to the uppermost part of the whorls, below suture, forming some elongated tuberculae; this is a tendency which becomes more conspicuous in the living species.

The characteristics of the material collected by Dr. Bristow at Loyola Formation (Lat. 78°52'W, Long. 2°34'S) in CM 46791, are as follows: axial incremental sculpture strong, 5 specimens; axial incremental sculpture conspicuous, 1; axial incremental sculpture less conspicuous, 10; axial incremental sculpture conspicuous at base, 1; axial incremental sculpture conspicuous on last whorl, 1; axial incremental sculpture conspicuous at top, 3; axial incremental sculpture not conspicuous, 4; spiral sculpture strong, 15; spiral sculpture conspicuous, 1; spiral sculpture not conspicuous (eroded), 8.

One full specimen with apex (37 by 15 mm, aperture 14 by 9 mm) which is a little more than half of the whorl, has the columellar lip slightly curved to right, forming angular base. In one specimen, the last whorls only are wider being 17 mm.

In the British Museum collection (G 55394-6) were observed 36 specimens from (probably) Shepard's original lot, plus many others collected by Dr. Bristow from Mangán CRB 36a, and from Basal Loyola, 2, 5, 8, 14, 17, 18a-b, 28.

Doryssa corrosensis (Pilsbry and Olsson, 1935:12, pl. 2, fig. 89), originally described as *Hemisinus* (see Parodiz, 1969:136), was indicated as being from Mangán Formation by Roberts (1975:261) and Bristow and Hoffstetter (1977:194), according to a preliminary report by Parodiz. Such identification must be corrected here, because those Miocene specimens belong to the common *D. bibiana*. *D. corrosensis* is an ?Eocene species from Los Corros Formation at Rio Sucio, Colombia (type in Academy of Natural Sciences, Philadelphia). Recently Boss and Parodiz (1977:118, figs. 10-11) reported *D. corrosensis* from Peru in the vicinity of Yarina on the Huallaga River, and its collector Dr. Bryan Patterson indicated the strata as early Tertiary (mid- or late Eocene), thus this species had a wide range from Colombia to Peru in the early Tertiary but not in the Miocene.

Genus *Paleoanculosa* Parodiz

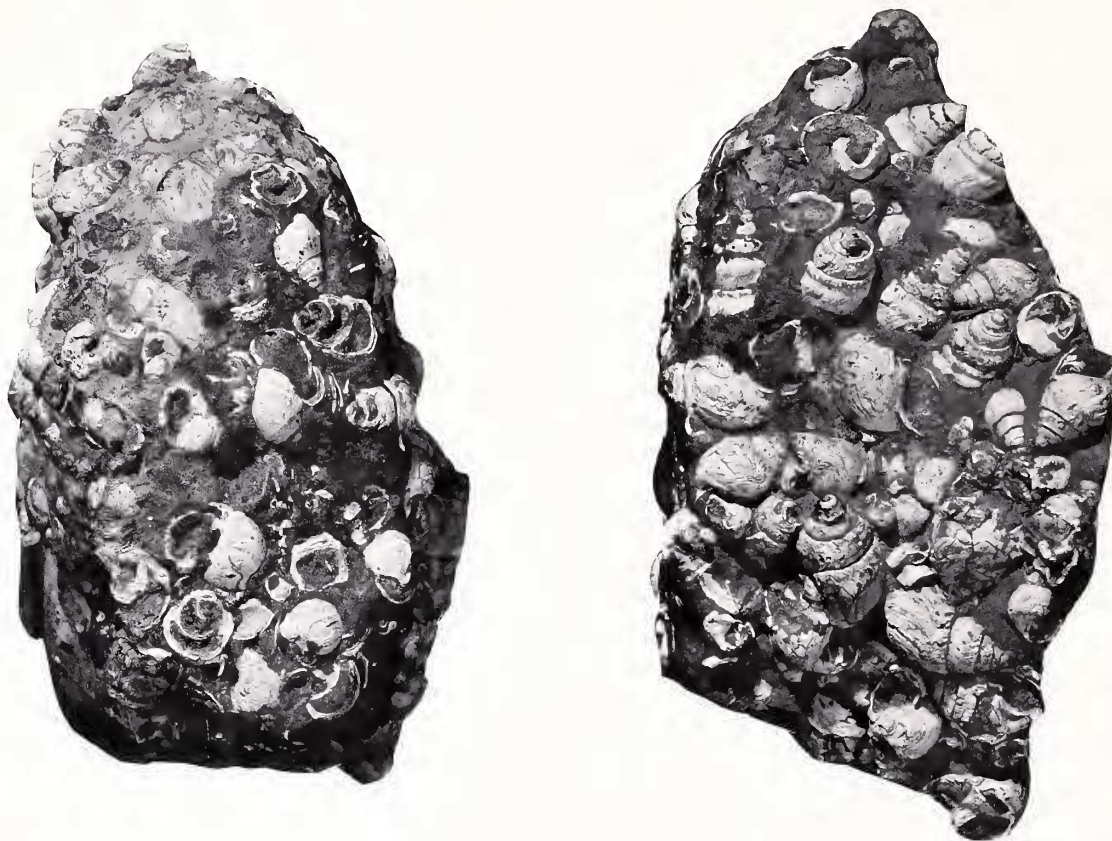
Type species.—*P. patagonica* Parodiz, 1969:124, pl. 14, figs. 3-4.



Fig. 19.—*Paleoanculosa kennerleyi*, new species (holotype, CM 46792). Near (east) Biblián, Mangán Formation. $\times 6$.

Shell with large body whorl, spire short and conical. Sutures well defined. Body whorl depressed about the middle. Upper part of the whorls subgrate or shouldered. Columella thickened by a callus. The general appearance recalls that of the living "*Anculosa*" (= *Leptoxis*) from the southern United States. The species previously known of this fossil group were described as "*Melania*" or "*Paludina*" from the early Tertiary of southern South America (Argentina and Chile). The largest one, *P. macrochilinoidea* (Doello-Jurado), has a certain resemblance to *Hannatoma*, but this genus is a Thiaridae. The most abundant species, *P. bullia* (Ihering), from the Paleocene of Patagonia is slender and less shouldered, angulated at the base and perhaps represents a subdivision of the group.

The following new species is the only one known from northern South America and the Miocene.



Figs. 20–21.—Conglomerates of Mangán Formation, with *Paleoanculosa kennerleyi*, new species (paratypes, CM 46793). Natural size.

Paleoanculosa kennerleyi, new species

Figs. 19–21

Holotype.—CM 46792, CRB 20, Lat. 78°53'45"W, Long. 2°45'16"S (a short distance east of Biblián and 6 km WSW Azogues) in strata of Mangán Formation, Upper Miocene-Eocene.

Paratypes.—40 in CM and 60 in British Museum from the type locality. Other paratypes from 20 km north, Lat. 78°52'30"W, Long. 2°34'09"S, CM 46793. Apart from those individually separated specimens, many others are contained in matrix conglomerates.

Description.—Shell ovoid-conic, that is, the spire above the last subsutural cord is decidedly pyramidal, while the last whorl below that cord is very convex and ovate. Five and a half to six whorls, the first one and a half regularly convex constitutes the nucleus which is flat; the following whorls increase rapidly and regularly as to give a wide base to the spire which is one-third of the total length. The sides of the whorls on the spire are flat, although they might give the impression of being somewhat convex because of a wide spiral ridge running across the lower half of each whorl down to the penultimate one. On the last body whorl, which is very wide and rounded, the ridge is at the top,

below the suture, ending at the lip, and leaves a marked canaliculation between it and the remainder of the whorl. The body whorl is two-thirds of the total length, and as wide as high. The suture is well impressed, giving to the spire a gradate aspect. All the whorls, except at the apex, are noticeably marked by sigmoid incremental lines; there are no other sculptural features. The aperture occupies half of the length of the shell and begins at a short distance from the ridge of the last whorl; peristomatic area broken in most specimens but there is indication of the outer lip being thin. The columellar wall is widely round and ends abruptly into a very short canal which is very slightly deflected to the right. On the posterior side of the body whorl the incremental sculpture is stronger, forming very elongated S's. The posterior end of the canal is roundish and a little protractive. The umbilicus appears closed or very narrowly rimated.

Dimensions of holotype.—Length, 22.5 mm; diameter, 12 mm; spire, 10.5 mm; length of last whorl, 12 mm; penultimate whorl, 2.9 mm high. The spire forms an angle of 65° in relation to the axis.

Comparisons.—Compared with other species of *Paleoanculosa*, *P. kennerleyi* has a more conical spire which is wider at the base, the body whorl more globose, and the incremental lines stronger, with the depression on the upper part of the body whorl deeper than in the older *P. macrochilinoides*.

Remarks.—The species is named in memory of Brian Kennerley, leader of the British Geological project in Ecuador, who died tragically in a car accident during a sojourn in Colombia. Specimens of this species were previously reported by Pilsbry and Olsson (1935, as *Aylacostoma sigmachilus*) and Bristow and Hoffstetter (1977:195, as *Aylacostoma* (*H.*) *sigmachilus*).

Some specimens are a little more elongated and narrower than the type (22.5 mm by 9.5 mm) and others are shorter and wider (13 mm). These proportions are of specimens that still preserve parts of the shell. Internal casts, of course, show whorls apparently more convex and more gradated. In a few specimens there are indications of three basal cords, but this is a juvenile character which is absent in fully-developed specimens. Some specimens show deformities caused by diastrophic pressure as is seen in many other species in the same strata.

Family Thiariidae

The separation of the living Thiariidae from the Pleuroceridae is based on the reproductive system, the first being considered to be parthenogenetic, although there are not enough studies to prove that all forms in the family are so. The shells may show characters convergent with the Pleuroceridae, increasing the difficulty to distinguish the families when the study is on fossils. The systems used by Pilsbry (1944), Morrison (1954) and Wenz (1938) are followed here.

Subfamily Aylacostominae

Hemisinucae Wenz, 1938.

Genus *Aylacostoma* Spix, 1827

Type species.—By subsequent designation Morrison (1954)—*Aylacostoma glabrum* Spix, = *Melania scalare* Wagner, 1827.

Most of the shells in *Aylacostoma* (sensu stricto) are turritelliform, with flat-sided whorls and spirally ribbed, and angular at the base. The genus ranges from Central America to South America in Brazil and northern Argentina; they are divided in several subgenera but the Ecuadorian Miocene species are *Aylacostoma* (s.l.).

Aylacostoma sulcatus Conrad, 1871

Hemisinus sulcatus Conrad, 1871, Amer. J. Conchology, 6:194, pl. 10, fig. 2.

Semisinus sulcatus, de Greve, 1938: pl. 4, figs. 17–19, 21–24.

Type locality.—“... near Pebas (or 30 miles below Pebas) in strata that cannot be later than Tertiary.”

Materials examined.—Locality CRB 42, Mangán Formation, middle Miocene. Abundant; found in shales with *Neocorbicula cojitamboensis*.

Original description.—“Subulately turbinated, solid, polished, whorls slightly convex, revolving grooves or impressed lines not closely arranged, about six on the penultimate whorl, and two minute lines, one towards each boundary; last whorl with about 23 lines, reach the base. An elegant species closely allied to *H. tenellus* Reeve [from Pernambuco] but it has a longer last whorl and narrower aperture.” Conrad gave no dimensions, but the figure, which is of natural size, measures 26 mm long, 10 mm wide, and the aperture is 11 by 5 mm; the aperture is noticeably angulated at both ends.

Remarks.—An extremely variable species of which one variation is represented by Conrad's figured type, for which he indicated a polished surface, “elegant” appearance, and not too close and not too impressed revolving lines. It is very clear that Conrad did indicate real cords or ribs; 17 specimens in our lot correspond to this smoothish form. The largest is 25 mm long and 13 mm wide. The brevity of the description and the not very satisfactory figure, made de Greve comment (1938:100), “T. A. Conrad's, pl. 10, f. 2, makes its distinction not clear enough.”

A supplementary observation is here pertinent on details not included in the original description. The spiral lines are extremely fine and visible only under good magnification (which distinguishes it from other named *sulcatus* with strong ribbed spirals). It has numerous, regular but very fine, axial incremental lines which run from the sutures becoming undulate in the last whorl. Below the suture there is one, sometimes two, better-marked spiral lines crossing the axial lines of growth which at that point are more conspicuous; this gives to the sutural zone a margined appearance. The columella is curved, ending into a very short canal that does not extend beyond the basal lip. Also, the last whorl appears more elongated. It is possible that these specimens represent an allochronic and allopatric form, but because there is much variation in shape, as well as in sculpture, any nomenclatorial distinction would be of doubtful value.

Another form in the same lot is represented by one specimen that differs more from Conrad's description. It is more turreted with stronger spiral lines so as to form, on the upper part of the whorls, a cord-like sculpture, crossed by the weaker growth lines. In the body whorl there are two cords on the

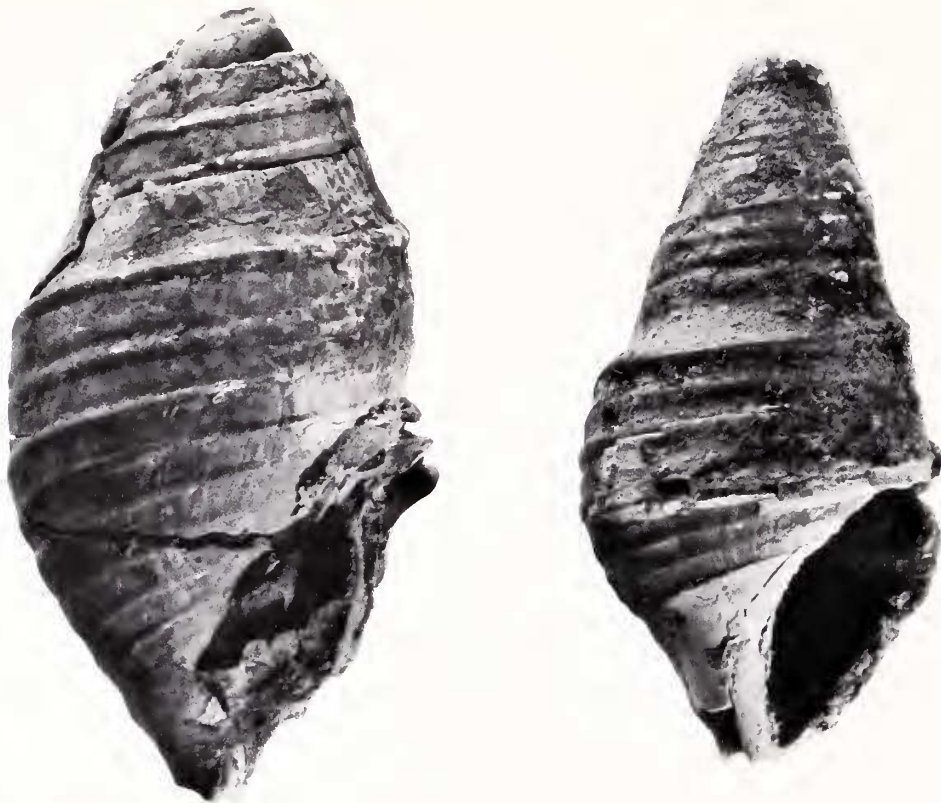


Fig. 22.—Two specimens of *Aylacostoma browni* from Middle Mangán Formation. $\times 5$. The species is also found at the Loyola Formation, where most of the specimens are diastrophically deformed.

upper part below suture, a smoother middle area with fine spirals and then, from the periphery, which is somewhat angulated, to the base, about 10 spiral ridges crossed by extremely fine incremental lines. This individual is similar to those figured by de Greve (pl. 4, figs. 17, 19, 21–22, 24–25) as “*Semisinus*” *sulcatus* from Iquitos, Peru, in the Pliocene.

Other variations illustrated by de Greve have strong axial riblets and revolving lines over the whole surface. However, those of pl. 4, fig. 18 and text fig. 23, are not *sulcatus*, and actually belong to the following species, *A. dickersoni* (Palmer).

Aylacostoma dickersoni (Palmer)

Semisinus sulcatus (Conrad), de Greve, 1938, pl. 4, fig. 18 and text fig. 13 (non *sulcatus* Conrad).

Hemisinus peyeri dickersoni Palmer, in Liddle and Palmer, 1941: 398, pl. 6, figs. 15–18.

Aylacostoma (*Longiverena*) *peyeri dickersoni*, Parodiz, 1969:149.

Type locality.—Arroyo Potrero, west of Cojitambo, Cuenca vicinity, in bituminous limestone (this corresponds to what is now recognized as Loyola Formation, and the same loc. of *Neocorbicula cojitamboensis*).

Remarks.—Described as a new variety of *peyeri*, the author said (Palmer, in Liddle and Palmer 1941: 399) that “this ‘species’ is related to *Hemisinus peyeri* (de Greve)”; “*Semisinus*” *peyeri*—as originally described—is from the Pliocene of Iquitos, Peru, and it has less nodulous ribs with narrower interspaces. *Aylacostoma paleus* (Pilsbry, 1950) is similar in shape but differs by the absence of tubercles on the ribs, and it is from the Oligocene of Peru. According to Pilsbry *A. peyeri* and *A. dickersoni* are different species, as well as of different age. For convenience these species were assigned to the group *Longiverena*; however, subgeneric divisions in *Aylacostoma* still need clarification.

The material of *A. dickersoni* collected by Bristow is from the locality CRB 1, Basal Azogues.

Aylacostoma browni (Etheridge, 1879)

Fig. 22

?*Melanopsis browni* Etheridge, Quart. J. Geol. Soc., London, 35:87, fig. 5. Oliveira Roxo and Leonardos, Geol. Brasil, 1943:631, pl. 29, fig. 19.

Semisinus sulcatus, de Greve (in part), 1938: fig. 18, pl. 4, and text fig. 19.

Aylacostoma sulcatus, Parodiz (in part), 1969:141, pl. 14, figs. 6–7.

Paleoanculosa cf. *bullia* (Ihering), Bristow, 1973:30.

Paleoanculosa sp. Bristow and Hoffstetter, 1977:194.

Type locality.—Canama, Brazil. All the species collected by C. B. Brown and described by Etheridge are from Canama. In the title of the paper Etheridge indicated “Tertiary deposits of Solimoes and Javary rivers”; Canama is not on the banks of these rivers, but on the Curuça River which is 85 mi east of the Javary and the Peruvian border. Oliveira Roxo and Leonardos (1943) reported the species from Tres Unidos, on the Javary. The Curuça River is a tributary of the Javary, but the confluence is farther north, at Caixas.

Original description.—“Shell turreted, elongated; whorls five, sides vertical; sulcus or suture at junction of the whorls depressed, the sutural edge elevated; upper whorls double carinated; body whorl concentrically banded by nearly equidistant lines, slightly rugose at the base, here and there possessing a varice; anterior canal slightly notched; outer lip toothed; columellar lip slightly reflected and thick. This shell resembles *Melania*, and but for a siphonal notch could be referred to that genus or the subgenus *Plotia*.”

The author also remarked that he had several specimens but nothing to compare with them, and that the species was, apparently, like the other remains from the Amazon Valley, estuarine in habit. The localities on the Javary and Solimoes are probably Pliocene.

Remarks.—Twenty specimens, CM 46804, from locality CRB 42 (the same that contains the many *A. sulcatus* and *Neocorbicula*) plus numerous fragments in matrix or loose, made it possible to identify this species and correct the indication in my paper of 1969 (p. 141) where it was synonymized under *A. sulcatus*. The specimens referred to on that occasion were received from the Geological Service of Brazil from the locality Tres Unidos, on the Javary River, and were labelled “*Hydrobia* (*Conradia*) *lindea* Conrad.” Etheridge’s original illustration of the species, although recognizable, was not very accurate, and I figured the specimens from Tres Unidos (pl. 14, figs. 6–7) as *sulcatus*, but actually they are typical *browni*.

The spiral sculpture is very regular all over the shell and the spire is very pointed and appears as “inserted” on top of the body whorl, forming there a well-defined flat shoulder. The crenulations indicated for the outer lip correspond to the ending of the spiral cords. There are no visible axial lines. Younger individuals are rather slender, and the spire slightly scalated; adults are always broader.

The Miocene specimens collected by Bristow are



Fig. 23.—Conglomerate from Loyola Formation with A) *Dor-yssa*; B) *Potamolithoides*; C) *Aylacostoma*; D) *Gyraulus*(?); E) *Hydrobia*(?). Natural size.

generally larger than those known from the Pliocene of Brazil, and the spiral sculpture may not be as regular as in typical *A. browni*. As in other species, they may represent an older ancestral race, or allochronic subspecies, but until more and better materials for comparison are found, they remain indicated, in a broad sense, as *A. browni*. Most of the specimens have been deformed by diastrophic pressure.

This species was also found by Bristow at Loc. CRB 36, which corresponds to mid-Mangán, and in sediments of Lower Miocene of Basal Loyola, CRB 18 (Fig. 23). Apparently, it had a wide range during all the Miocene in Ecuador.

The average size of specimens of *A. browni*, which had not been diastrophically deformed, is 20–22 in length and 11 mm wide.

Aylacostoma sp.

From the locality CRB 42 (Mangán), there is a very large and elongated specimen that is very close and possibly just a variation of *A. browni*. It measures 31 mm in length with the apex broken (entire

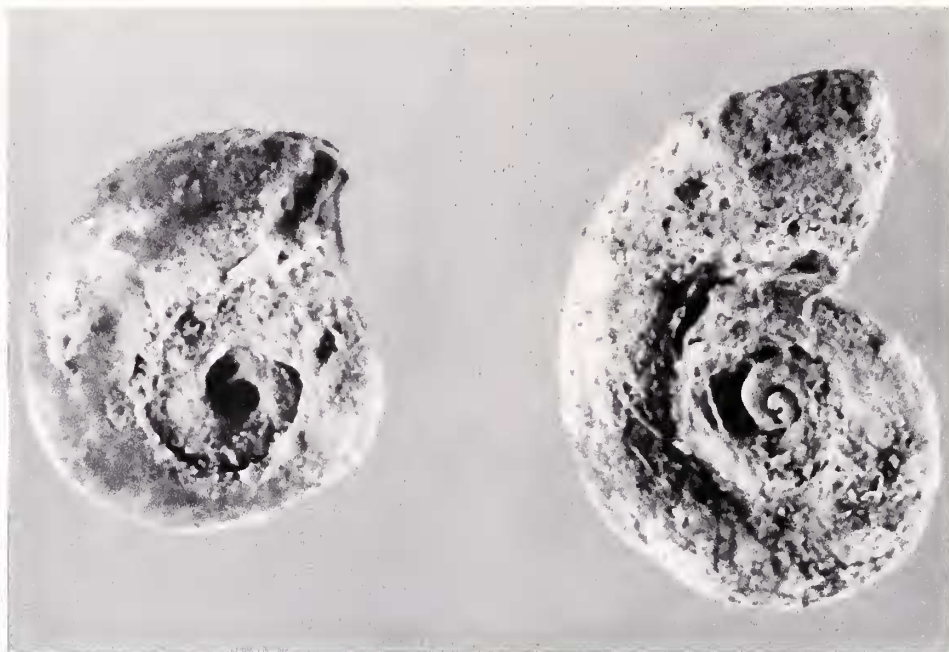


Fig. 24.—*Gyraulus* sp. Basal Azogues Formation. Carnegie Museum specimens. $\times 20$.

it must have been more than 35) and the width of the last whorl is 15 mm. The spiral sculpture on the last whorl is very regular, and 17 spiral cords can be counted from the sutural shoulder to the base. Apart from the size and the appearance of being more shouldered, all other characteristics are the same as in *A. browni*. The reddish Mangán shales that contain this form are also abundant in *Neocorbicula*.

Order Pulmonata
Superfamily Lymnaeacea
Family Planorbiidae
Genus *Gyraulus* Charpentier, 1837

Fig. 24

From locality CRB 7 (Basal Loyola), there are casts of a very small planorbid (about 2.5 mm in diameter) that probably corresponds to *Gyraulus*, as Roberts indicated (1975, *Gyraulis*), but it can be compared also with *Armigerus*, therefore the assignation here is only tentative. There are *Gyraulus* known from the Cretaceous-Paleocene of Europe and North Africa, and from the Miocene of Germany, *G. trochiformis* (Stahl). Planorbids from the Tertiary of South America, however, are known to belong to the genus *Taphius*.

The shell is very flat, angulated at periphery, with approximately four whorls, the last one (just broken

behind peristome) about three times as wide as the penultimate; the growth from the nuclear whorls is very rapid. The suture is well impressed. The aperture is oval, elongated, and narrowed at the end.

Superfamily Succineacea
Family Succineidae
Genus *Succinea* Draparnaud, 1801

Several fragments of an unidentifiable *Succinea* in limestone from locality KB 1, which contains also small Sphaeriids bivalves. Roberts has indicated *Succinea* for CRB 7 (Loyola).

Incertae Sedis

In a piece of coarse conglomerate of Basal Loyola (CRB 7) was observed a specimen of organic remains, like a very tenue roundish valve compressed into the matrix. Under the microscope it looks like a left valve of some minute pectinid, like *Propeamusium*, on account of having 12 equally-spaced radial ribs and an auriculated expansion at the top. A more careful observation reveals the unlikeliness of such an assumption; it probably represents an unidentified fish scale. It measures 3.5 mm at its widest diameter. It was probably deposited in shallow water into which other, freshwater organisms, like Hydrobiidae, and others have been drifted.

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